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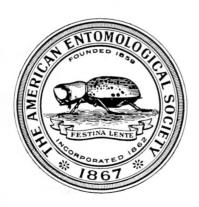


MEMOIRS OF THE AMERICAN ENTOMOLOGICAL SOCIETY NUMBER 21

A TAXONOMIC AND ZOOGEOGRAPHIC SURVEY OF THE SCARABAEINAE OF THE ANTILLES (COLEOPTERA: SCARABAEIDAE)

BY

ERIC G. MATTHEWS



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Dedicated to the Memory of the late Harold J. Grant, Jr.



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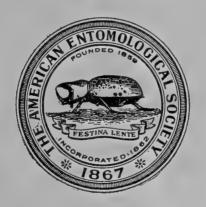
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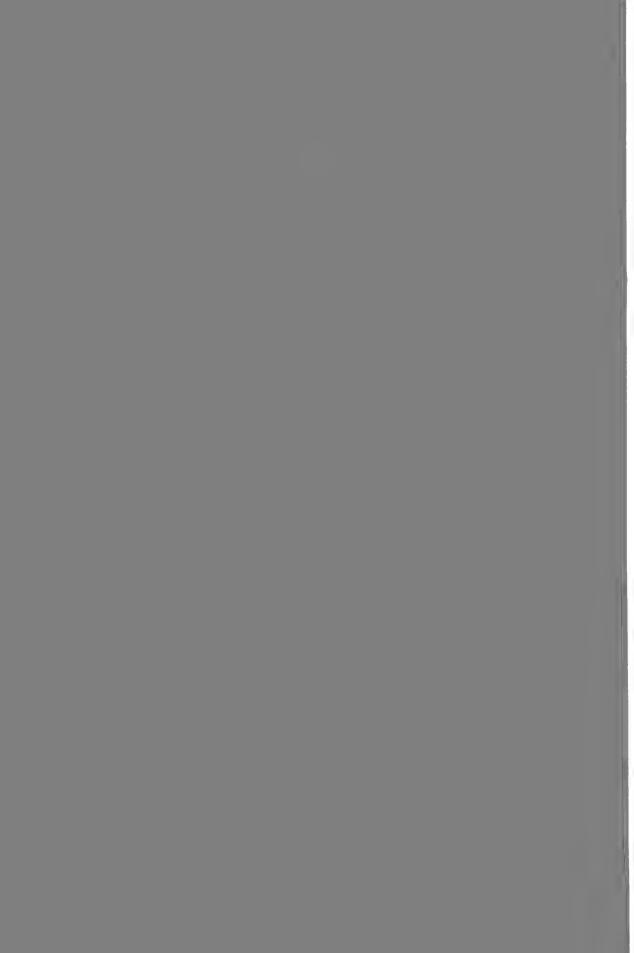
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The present paper is the first comprehensive revision of the scarabaeine dung beetles of the Greater and Lesser Antilles in the strict sense (not including Caribbean islands of continental origin). In order to carry out this study the author looked for Scarabaeinae on the islands of Jamaica, Hispaniola (Dominican side), Puerto Rico, St. Thomas, Ste. Croix, St. Martin, St. Christopher, Guadeloupe, Dominica, Martinique, St. Lucia, St. Vincent, Bequia (Grenadines), and Grenada. Borrowed material was examined from some of the above islands and from Cuba, Haiti, Montserrat, Mustique, Union, and Carriacou (Grenadines). The Van Voast-American Museum Expedition material from the Bahamas was also examined. All islands of the Caribbean area which are not mentioned above must be considered to be not included in this survey.

¹ Supported by grant No. 3600 from the Penrose Fund of the American Philosophical Society and grant No. GB-3581 from the National Science Foundation. Publication costs were largely defrayed by grant No. GN-548 from the National Science Foundation, and in part by the American Entomological Society.

INTRODUCTION

The earliest species of Scarabaeinae to be reported and described from the Antilles were those commonly found in cattle dung in Jamaica, Cuba, and Hispaniola. One of these — Phanaeus carnifex (Linnaeus) of Jamaica — even figures in the Systema Naturae and earlier works, such as Brown (1756). The first important island faunal survey involving scarabs and other beetles was that of Chevrolat (1862) on Cuba; this did not describe any new Scarabaeinae, however. To the Cuban naturalist Johannes Gundlach we owe the first discovery of the small canthonine genera Canthonella and Canthochilum, three species of which were described by Edgar von Harold in 1868 and 1869 (as Canthon). The next important milestone in Antillean scarabaeine studies was the publication of Fleutiaux and Sallé's "Coléoptères de la Guadeloupe" (1889 and subsequent supplements) on the basis of material amassed by the resident collectors Delauney and Vitrac. This work marks the first record of the canthonine genus *Pseudocanthon* in the Antilles (described as *Canthon* vitraci Fleutiaux and Sallé) and the first record of the genus Ateuchus (=Choeridium). In the years 1889-1891 H. H. Smith collected on Grenada and St. Vincent and his laparostict material was described by G. J. Arrow in 1903. This work included a number of new species and records, including the first record of the genus Uroxys from the Antilles. Thereafter there was no new activity until the collection of a number of species of the genera Canthonella and Canthochilum in Puerto Rico by F. E. Lutz, A. J. Mutchler, and the resident agricultural entomologist R. G. Oakley, as reported by E. A. Chapin (1930, 1934, 1935). Chapin was the first to recognize the uniqueness of these small scarabs and to describe them as representatives of new genera. This also marked the first time these genera had been re-collected since Gundlach's early Cuban captures. From 1935 to 1937 R. E. Blackwelder collected extensively in the Antilles. His scarabaeine material, which did not include any new species, is recorded here for the first time. Some time later, Fleutiaux, Legros, Lepesme, and Paulian (1947) published the first part of a survey of the Coleoptera of the French Antilles. The scarab portion, written by Paulian, is unfortunately based on little more material than was available to Fleutiaux and Sallé in 1889. In this work Paulian de-

scribed a genus Opiocanthon to receive Canthon vitraci Fleutiaux and Sallé. In the present work Opiocanthon is considered to be a synonym of Pseudocanthon. Next came Martínez's (1954) re-examination of Canthonella, Pereira and Martínez's (1956) description of a genus Nesocanthon to receive the Hispaniolan species previously in Canthon (and returned to Canthon in the present study), and the present author's activities, which began in 1962 with a life-history study of a species of Canthochilum in Puerto Rico (Matthews, 1963). This was followed by a survey of the taxonomy and distribution of the species of Canthochilum and Canthonella in Puerto Rico (Matthews. 1965). Simultaneously, F. de Zayas was collecting small canthonines in Cuba by the Berlese funnel method and thus discovered a number of new species, described in a recent paper (Zayas and Matthews, 1966). In 1964 and 1965 the present author extended his activities to include most of the Antillean region.

Blackwelder (1944, 1957) listed 29 species of Scarabaeinae from the Antilles other than Trinidad. One additional species and three subspecies were described by Matthews (1965) and six additional species by Zayas and Matthews (1966). The present paper describes 10 new species and one new subspecies, one name in synonymy is resurrected as a subspecies, and three previously known species are recorded from the Antilles for the first time. One specific name is synonymized and eight species are removed from the Antillean list. This brings the total to 40 species and five subspecies of Scarabaeinae known from the Antilles at present.

The generic names *Opiocanthon* Paulian and *Nesocanthon* Pereira and Martínez are here synonymized with *Pseudocanthon* Bates and *Canthon* Hoffmannsegg respectively. The genus *Drepanocerus* Kirby is recorded from the Antilles, and from the Western Hemisphere, for the first time.

METHODS

The present study is based on an examination of 967 specimens borrowed from museums and private collections and 1,072 specimens collected by the author outside of Puerto Rico. 1,964 specimens collected in Puerto Rico have previously been reported on (Matthews, 1965). All new taxa and new records, except one, are based on the author's own collecting. The author personally examined all of the

species recorded from the Antilles and collected in the field 31 of the 45 taxa known from the area.

The principal collecting method used was that of the dung-baited trap, consisting of a glass jar embedded in soil up to the rim and covered by a leaf to keep out rain. These traps are left approximately 24 hours before being picked up. This method works only in forests, but it is the forest species which are of greatest interest and importance. The Antillean islands were originally almost entirely covered with forests of various types. Traps were set in all major forest types (as discussed in the part on zoogeography) and at representative altitudes, whenever possible. The bait, placed in the bottom of the jar, was initially cow dung, used successfully in Puerto Rico (Matthews, 1965), but results proved disappointing and it soon became clear that the beetles have to be present in very large numbers (as in Puerto Rico) for cow dung to be an effective attractant. Human excrement was then adopted as the principal bait and was found to be far more effective. In at least one location on each island a dead lizard or snail was also used. This revealed any necrophagous tendencies among the species present, but did not collect any species which did not also come to excrement. Rotten fruits on the ground were examined at every opportunity, but did not yield any Scarabaeinae.

It is the author's opinion, based on his experience, that food specialization is rare among scarabaeine dung beetles. Saprophagous, necrophagous and mycetophagous specializations are sometimes seen, but far more important ecologically are other environmental factors such as microclimatic and vegetational features, which generally limit the species to certain habitats. Within these habitats they will usually feed on a wide range of excrements (if available) and often also on carrion. It is therefore not necessary to use a wide selection of baits when trapping. On the other hand, it is essential to set traps in as wide a range of forested habitats as possible. On an island, this may be done by setting traps along two or three vertical transects, since (at least in smaller islands) the species seem to range themselves in horizontal altitude distribution "belts" rather than in patchwork zones, in correlation with the distribution of the plant communities.

While major effort was concentrated on forests, pastures at various altitudes were also examined for species which might be capable of invading this artificial environment. Very few species were found

in pastures which did not also occur in xerophytic forests, among these were two species of *Onthophagus* introduced by man on Martinique.

All illustrations are by the author. Complete synonymies are not given for taxa which also occur outside of the Antilles. Types designated as "not found in MNHN" are those which should be in the Paris Museum but which could not be found recently when sought by Dr. R. Descarpentries.

ACKNOWLEDGMENTS

The author wishes to thank the curators of the following collections for lending material for examination.

BMNH — British Museum (Natural History), London (Dr. R. D. Pope).

FZ — Collection of Ing. F. de Zayas, Havana.

GH — Collection of Dr. Gonzalo Halffter, Mexico City.

INHS — Illinois Natural History Survey, Urbana (Dr. M. W. Sanderson).

MNHN — Muséum National d'Histoire Naturelle, Paris (Dr. R. Descarpentries).

RP — Collection of Father R. Pinchon, Fort-de-France.

SM!J — Science Museum, The Institute of Jamaica, Kingston (Dr. T. H. Farr).

USNM — United States National Museum, Washington (Mr. O. L. Cartwright).

ZLRU — Zoologisch Laboratorium der Rijksuniversiteit, Utrecht (Dr. P. W. Hummelinck).

ZMHU — Zoologisches Museum der Humboldt-Universität zu Berlin (Dr. F. Hieke).

All new holotypes are deposited in USNM. All remaining material collected by the author is deposited in some of the above collections (as designated under each species) and in some of the following additional collections:

AM — Collection of Dr. A. Martínez, Buenos Aires.

ANSP — Academy of Natural Sciences, Philadelphia (Dr. H. J. Grant, Jr.).

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CNC — Canadian National Collection, Ottawa (Dr. H. F. Howden).

Particular thanks are due to Drs. R. Descarpentries and R. D. Pope for having sorted and sent the important Antillean material from the collections in their care.

Several colleagues willingly helped with the numerous taxonomic, nomenclatorial, and distributional problems which arose, thus greatly enhancing the value of the present work. They are O. L. Cartwright (Washington), W. D. Edmonds (Lawrence), G. Halffter (Mexico City), H. F. Howden (Ottawa), B.-O. Landin (Lund), A. Martínez (Buenos Aires), R. Pinchon (Fort-de-France), R. D. Pope (London), R. Woodruff (Gainesville), and F. de Zayas (Havana).

The author's collecting on several islands was greatly facilitated by the guidance of the following temporary or permanent residents of the islands indicated: Mr. Bernard Diederich (Dominican Republic), Dr. T. H. Farr (Jamaica), Dr. O. S. Flint (Dominica), and Father R. Pinchon (Martinique).

Finally, grateful acknowledgment is made to the Smithsonian Institution for having made available to the author the facilities of the Bredin-Archbold-Smithsonian Biological Survey of Dominica during the author's stay on that island in 1964.

PART I. TAXONOMY

Key to the Genera of Scarabaeinae of the Antilles

1.	Middle and hind tibiae slender, apically only moderately widened or
	not at all; head and pronotum always devoid of tubercles or strong
	carinae (Tribe Scarabaeini)
1'.	Middle and hind tibiae abruptly and strongly widened apically; head
	and pronotum often with strong carinae or other projections 5
2(1).	Prothorax below anteriorly not excavated; propleurae without a trans-
	verse carina running from coxal cavity to lateral margin; posterior
	edge of head margined. Hispaniola, Grenada
2'.	Prothorax below anteriorly excavated to receive fore femora, the ex-
	cavation bounded posteriorly by a transverse carina; posterior edge of
	head not margined

3(2').	Dorsal surfaces densely pilose; clypeus bidentate; pronotum basally mar-
	gined; tarsal claws basally toothed. Cuba, Hispaniola, Puerto Rico
3'.	Dorsal surfaces glabrous or with extremely short hairs; clypeus with
	more than two teeth; pronotum basally not margined; tarsal claws
	basally angulate but not dentate
4(3').	Mesosternum very long, only about four times as wide as long; meso-
	metasternal suture marked by a fine margin which often bends back
	laterally to form broad inner mid-coxal margins; mentum not deeply
	emarginate; second segment of labial palpi longer than first. Cuba,
	Puerto Rico
4'.	Mesosternum shorter, 5-8 times as wide as long; inner mid-coxal margin
	narrow; mentum deeply emarginate; second segment of labial palpi
	shorter than first. Jamaica, Lesser Antilles Pseudocanthon Bates.
5(1').	Basal segment of antennal club enveloping the other two; tarsal claws
	absent (Tribe Coprini, Subtribe Phanaeina). Jamaica
5'.	All antennal club segments free; tarsal claws present
6(5').	Second segment of labial palpi larger than first, the third segment min-
	ute, difficult to see
6'.	Second segment of labial palpi smaller than first, the third segment
	clearly visible (Tribe Coprini, Subtribe Dichotomina) 9
7(6).	Antennae 9-segmented (Tribe Onthophagini). Cuba, Hispaniola, Lesser
	Antilles Onthophagus Latreille.
7'.	Antennae 8-segmented (Tribe Oniticellini)
8(7').	Dorsal surfaces densely covered with short, very stout hairs; scutellum
	normally not visible; elytra covering sides of abdominal sternites
	above. Jamaica
8'.	Dorsal surfaces largely glabrous; scutellum visible; elytra leaving sides
	of abdomen exposed above. Jamaica, Cuba, Bahamas
9(6').	Lateral foveae of pronotum round. Lesser Antilles Ateuchus Weber.
9'.	Lateral foveae of pronotum in form of longitudinal grooves. Lesser
	Antilles

Genus ONTHOPHAGUS Latreille

Onthophagus Latreille, 1802, Histoire naturelle, générale et particulière des crustacés et des insectes, Vol. 3, p. 141.

Type of Genus. — Scarabaeus taurus Schreber, 1759.

Description. — Size and form highly variable. Second segment of labial palpi a little larger than first, the third segment minute. Antennae nine-segmented, the club lamellae separate. Vertex without backwardly directed lamella. Base of pronotum strongly rounded or slightly angulate medially, its

dorsum often strongly convex. Scute!lum nearly always absent. Elytra apically evenly rounded, with eight striae, without intercalary striae. Distal edge of fore tibiae and apical tooth clearly oblique, not forming a right angle with inner edge. Fore tibiae with four outer teeth, rarely three. Middle and hind tibiae strongly dilated apically. Tarsi always with five segments, claws always present, four hind tarsi not greatly widened or shortened. First hind tarsal segment greatly elongated, linear.

Distribution. — World-wide (\pm 1,500 species). In the Antilles (5 species): Cuba, Hispaniola, Grenada, Grenadines, St. Vincent, Martinique, Dominica, Guadeloupe. Here recorded for the first time from the Grenadines, Martinique, and Dominica.

Remarks. — This is the only genus of the tribe Onthophagini in the Western Hemisphere and it is of Ethiopian origin (Balthasar, 1963). From their distribution, the American species appear to have entered from Asia via the Bering Bridge into North America very early in the Cenozoic, as there is a moderate radiation in South America (Halffter, 1964). Penetration into the Antilles has been minimal, only three native species occurring there, one having invaded from South America up the Lesser Antilles, the other two being derived from a common ancestral species which invaded the Greater Antilles from an unknown direction. Two additional, introduced species are reported here for the first time, both from Martinique.

Key to the Species of Onthophagus of the Antilles

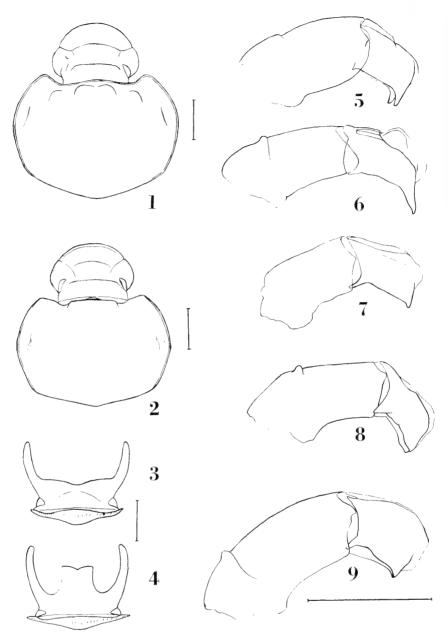
- 1. Dorsal surfaces entirely densely covered with short, very stout bristles, these arranged in close-set double or triple rows on elytral intervals; head and pronotum unarmed in both sexes; elytra with a symmetrical dark pattern on a yellow background (fig. 13). Martinique, Africa bituberculatus (Olivier).
- 1'. Dorsal surfaces glabrous or with finer setae; head and pronotum armed in both sexes, at least with strong carinae; elytra may be bicolored, but never with a dark symmetrical pattern set on a yellow background

- 5'. At least some punctures setigerous, especially along sides; interpunctural surfaces alutaceous to sericeous; ventral surfaces of femora pale yellowish, contrasting with darker body venter; dorsal surfaces of fore body with at least a trace of a metallic green tinge and elytra often with paler brown areas; abdomen often with yellowish infusion. Lesser Antilles to Guadeloupe, except St. Lucia antillarum Arrow.

Onthophagus marginatus Laporte de Castelnau

Onthophagus marginatus Laporte, 1840, Histoire naturelle des animaux articulés, Vol. 2, p. 87; Chevrolat, 1864, Ann. Soc. Ent. France, ser. 4, vol. 4, p. 410; Leng and Mutchler, 1914, Bull. American Mus. Nat. His., vol. 33, p. 438; Blackwelder, 1944, United States Nat. Mus. Bull. 185, p. 211.

Description. — Entirely bronzed except for antennal clubs, which are white, and extensive yellow areas along postero-lateral and posterior edges of elytra. Lateral edges of abdomen and pygidium paler than rest of body. Head round, edge of clypeus rounded, cephalic punctuation and sculpturing differing in the sexes. Pronotal surface fairly densely punctate with punctures of two distinct sizes, interpunctural surface shagreened, sericeous. Large punctures of anterior declivities and sides bearing long, strong setae. Only a faint trace of a median longitudinal sulcus. Pronotal sculpturing differing in the sexes. Meso-



Figures 1-9. Fig. 1, Onthophagus a. albicornis Palisot, \mathfrak{P} , fore body. In this and all subsequent illustrations, the straight line represents 1 mm unless otherwise indicated. Fig. 2, Onthophagus antillarum Arrow, \mathfrak{P} , fore body. Fig. 3, Onthophagus a. albicornis Palisot, \mathfrak{F} , front view of head. Fig. 4, Onthophagus a. capitatus Laporte, \mathfrak{F} , front view of head. Fig. 5, Onthophagus

sternum with a median anterior smooth spot, the rest very densely punctate and setose. Metasternum smooth except for sparse, coarse punctures bearing long setae on anterior half of median lobe and lateral lobes. Elytral striae shallow, very indistinctly punctate. Interstriae slightly convex, shagreened, intervals 1, 3, 5, and 7 with a median row of widely spaced tubercles each bearing a strong seta. Remaining intervals, except eighth, without tubercles or with very small ones, without setae. Eighth interval with several rows of setigerous tubercles. Epipleura sparsely punctate and setigerous. Abdominal sternites shagreened, with a row of setigerous punctures along basal edge of each sternite. Disc of pygidium finely shagreened, coarsely and sparsely punctate, each puncture bearing a strong seta. The punctures not grouped. Aedeagus with point of paramere salient (fig. 5), but not as much as in albicornis. Total length 6.0-8.5 mm.

Sexual dimorphism. - Male: Edge of clypeus rounded and reflexed. A low, transverse clypeal suture. From with a high, curved transverse ridge (fig. 10), no horns. Head surface shagreened, punctate and somewhat rugose before clypeal carina, some of the punctures bearing strong vertical setae. Surface simply punctate behind clypeal carina, completely smooth behind frontal carina. Median pronotal prominences in the form of two approximated, horizontal gibbosities very near anterior margin. Anterolateral surfaces of pronotum strongly and abruptly declivous, a conical gibbosity present just above lateral fossae of pronotum. Fore tibia of male somewhat longer than that of female and bearing at inner corner of distal edge a long brush of fused setae nearly as long as tarsus. Last abdominal sternite shortened medially. Female: Clypeal edge not reflexed, clypeal surface before transverse carina transversely rugose, bearing a number of vertical setae. Rest of head shallowly punctate, very finely so behind frontal carina. Frons with a straight, prominent carina between eyes. Pronotum with a low median transverse fold near middle of anterior edge, otherwise devoid of gibbosities. Fore tibiae without the brush of fused setae at distal end. Last abdominal sternite not shortened medially.

Type. — Cuba. Not found in MNHN.

Remarks. — This species is related to O. albicornis of Hispaniola, both sharing the features listed in couplet 2 of the key and a somewhat similar pronotal sculpturing in the male. The author has not collected this species personally.

marginatus Laporte, aedeagus. Fig. 6, Onthophagus a. albicornis Palisot, aedeagus. Fig. 7, Onthophagus antillarum Arrow, aedeagus. Fig. 8, Onthophagus batesi Howden and Cartwright, aedeagus. Fig. 9, Onthophagus bituberculatus (Olivier), aedeagus.

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Distribution. — Cuba.

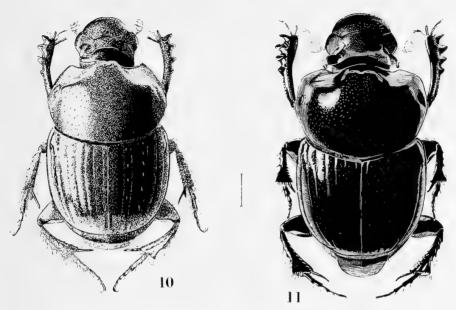
Material examined. — 201 specimens.

CUBA. Pinar del Río: San Vicente, 16 August 1959, R. E. Woodruff (4), [GH]; 9 July 1940, J. C. Bradley (10), [USNM]; June, 1948 (1), [USNM]; Paso Real de San Diego, Palmer and Riley (4), [USNM]; Cabanas, Palmer and Riley (1), [USNM]; Viñales, 4-6 June 1922, S. C. Bruner (1), [USNM]; Habana: Lag. Ariguanabo, June 1963, F. de Zayas (24), [FZ]; Santiago de las Vegas, 11 April 1905, G. Dimmock (4), [USNM]; S. C. Bruner (1), [USNM]; Havana, Baker (1), [USNM]; San Antonio de los Baños, J. H. Pazos (1), [USNM]; Santa Clara: Central Constancia, May 1914, J. F. Merrill (19), [USNM]; Camagüey: Baraguá, 5 May-11 June 1932 (96), [USNM]; 29 December 1925, D. L. Van Dine (1), [USNM]; 26-27 July 1927, C. F. Stahl, L. C. Scaramuzza, S. C. Bruner (1), [USNM]; Oriente: Vista Alegre, Santiago, 11 May 1940, C. T. Ramsden (4), [USNM]; location not determined: Soroa, Candelaria, 7 January 1962, A. Barrera (2), [GH]; Cayamas, E. A. Schwarz (23), [USNM]; Cabado, W. M. Mann (1), [USNM]; San Blas, Trinidad Mts., September-December 1931, G. C. Rowe (1), [USNM]; Río Almendares, 13 July 1916, [USNM]; Hoyo Colorado, M. C. Enamorado (1), [USNM]; no further data: Ex Musaeo Harold (1), [MNHN]; (2), [BMNH].

Onthophagus albicornis albicornis Palisot de Beauvois

Onthophagus albicornis Palisot, 1805, Insectes receuillis en Afrique et en Amérique, p. 25; Leng and Mutchler, 1914, Bull. American Mus. Nat. His., vol. 33, p. 438; Blackwelder, 1944, United States Nat. Mus. Bull. 185, p. 211.

Description. — Entirely shiny black except for antennal clubs, which are white, and some pale markings on distal elytral border above pygidium and on lateral edges of abdominal sternites. Pygidium with faint greenish tinge. Head round, edge of clypeus rounded, cephalic punctuation and sculpturing differing in the sexes. Last six antennal segments white in live individuals, yellowish in dead ones. Pronotal surface entirely, evenly, and very finely punctate, the punctures separated by far more than their diameter. Interpunctural surface glossy smooth, shiny. The punctures not setigerous. Only a faint trace of a median longitudinal sulcus. Pronotal sculpturing differing in the sexes. Mesosternum with a median longitudinal smooth line, the rest very densely punctate. Metasternum smooth except for punctures bearing long setae on lateral lobes and anterior part of median lobe. Elytral striae shallow, very indistinctly punctate. Interstriae flat, smooth, moderately and evenly punctate with very



Figures 10-11. Fig. 10, Onthophagus marginatus Laporte, &. Fig. 11, Onthophagus a. albicornis Palisot, &.

fine punctures, each bearing a very short seta, not apparent in worn specimens. Epipleura very sparsely punctate, the punctures setigerous. Abdominal sternites smooth, with a row of punctures bearing long setae along basal edge of each sternite. Pygidium finely but completely margined, the disc alutaceous, moderately and irregularly punctate and with an indistinct median longitudinal depression. A group of 4-6 punctures on either side bear long setae, remaining punctures not setigerous. Aedeagus with point of parameres drawn out (fig. 6). Total length 6.0-8.0 mm.

Sexual dimorphism. — Male: Edge of clypeus rounded and slightly reflexed. A fine, arcuate transverse clypeal suture present. Frons with two taurine horns emerging behind eyes and curving upward and backward, somewhat twisted (fig. 11). A very sharp, high, strongly sinuate carina joining horns across frons (fig. 3), this carina running up posterior surface of horns. Head entirely shallowly and finely punctate except behind frontal carina. Median pronotal prominences in form of a pair of approximated low gibbosities flanked by a flat lateral declivity, not a depression. Pronotum is proportionately slightly broader than that of female. Fore tibia considerably longer than that of female, the inner corner of distal edge bearing a long fused brush of setae nearly as long as tarsus. Female: Clypeal edge not reflexed, clypeal surface before transverse carina very densely punctate, rest of head finely punctate. Frons with an almost straight, prominent transverse carina between eyes. Pro-

notum with four nearly equidistant, prominent tubercles in a transverse row near anterior edge. Fore tibiae shorter than those of male, without the brush of fused setae at distal end. Last abdominal sternite not shortened medially.

Type. — Hispaniola. Destroyed.

Remarks. — The relationship of this species to *O. marginatus* of Cuba has been mentioned under the latter species.

That Palisot's *albicornis* is the Dominican (eastern) form of this species is shown beyond doubt by his figure of the male head in front view (fig. 3a opposite p. 23 of his "Insectes"), which shows the typical low, concave frontal carina as in fig. 3 of this work.

Ecology. — This is one of the most eurytopic of the Antillean species collected by the author. Although much commoner at low elevations, it was found up to 4,100 ft. It may be collected in both pastures and forests throughout its altitude range, in cow, horse, and human excrement. Very dry areas seem to be avoided. Exploitation of cow dung by this species and Canthon violaceus (Olivier) working together is intense at low elevations, where the ecological ranges of the two species coincide. Both are active in the heat of the day, and both share a very similar color pattern, including especially the white antennal clubs. The author believes that O. albicornis is a color mimic of Canthon violaceus because of these similarities in coloration and activity.

Distribution. — Dominican Republic.

Material examined.—35 specimens. The author's material is deposited in ANSP, BMNH, CNC, GH, MNHN, USNM.

HISPANIOLA. Dominican Republic. Distrito Nacional: 23 km NW of Santo Domingo on Santiago highway, 200 ft, 13 October 1964, E. G. Matthews (14); 30 km NW of Santo Domingo on Santiago highway, 200 ft, 14 October 1964, E. G. Matthews (5); Boca Chica, Sta. 41, 14 September 1935, R. E. Blackwelder (8), [USNM]; La Romana: La Romana, 9 April 1913, W. V. Tower (1), [USNM]; Puerto Plata: 10 mi SE of Puerto Plata, Sta. 36, R. E. Blackwelder (1), [USNM]; La Vega: Constanza, 3,600 ft, 14 October 1964, E. G. Matthews (2); 4 km N of Constanza, 4,100 ft, 13 October 1964, E. G. Matthews (1); Santiago: San José de las Matas, Sta. 38, 9 September 1935, R. E. Blackwelder (1), [USNM]; location not determined: San Francisco Mts., Aug. Busck (1), [USNM]; no further data: (2), [BMNH]; (1), [MNHN].

Onthophagus albicornis capitatus Laporte de Castelnau, new combination

Onthophagus capitatus Laporte, 1840, Histoire naturelle des animaux articulés, Vol. 2, p. 86; Gemminger and Harold, 1869, Catalogus coleopterorum, Vol. 4, p. 1024.

Description. — Differs from O. a. albicornis Palisot in the form of the head in both sexes. The clypeus of the male is broader, the anterior edge nearly straight, and the clypeo-genal angle deeper than in O. a. albicornis. The effect is to give the head a strongly squared-off appearance. Furthermore, the vertical transverse lamina between the head horns is strongly produced medially and bifid in major males (fig. 4). In minor males it is simply procurved and straight-edged in front view, never concave as in all a. albicornis. In the females, the frontal carina is correspondingly more prominent, strongly shelf-like, and directed forward.

In all other respects, including the form of the aedeagus, O. a. capitatus Laporte is identical to O. a. albicornis Palisot.

Type. — Saint Domingue. Not found in MNHN.

Remarks. — There can be no doubt that Laporte's capitatus is the Haitian or western form of this species, as his description clearly states: "Chaperon avancé, large, presque carré et offrant en arrière une forte carène transversale; tête offrant en arrière deux cornes assez courtes et arquées, et entre elles une élévation plate et bifide " (present author's italics).

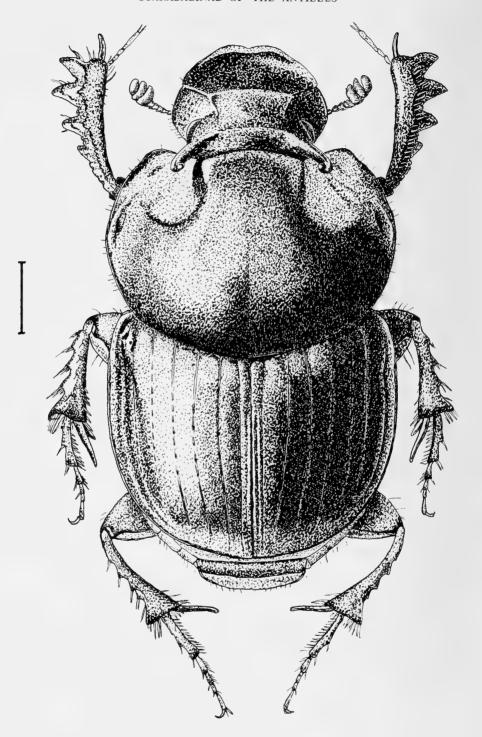
The author has not seen any intermediates between *albicornis* and *capitatus* and they may well be separate species. However, until their exact distribution and variation are worked out it seems best to treat them as subspecies in view of the close resemblance between them.

Distribution. — Haiti. The type locality of Saint Domingue should not be interpreted to mean what is now the Dominican Republic, as Saint Domingue is the former name of the entire island. All localities known for this subspecies are on the southern peninsula of Haiti or near Port-au-Prince. The altitude range is from sea level to 1,420 m (Kenscoff).

Material examined. — 43 specimens.

HISPANIOLA. HAITI: M. La Selle, Sta. 22, 8 August 1935, R. E. Blackwelder (8), [USNM]; 1.5 mi S of Kenscoff, Sta. 23, 23 August 1935, R. E. Blackwelder (15), [USNM]; Trouin, Sta. 24, 13 August 1935, R. E. Blackwelder (1), [USNM]; 5 mi S of Miragoâne,

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Sta. 27, 20 August 1935, R. E. Blackwelder (8), [USNM]; Kenscoff, 1 December 1946, G. N. Wolcott (1), [USNM]; Port-au-Prince, R. J. Crew (8), [USNM]; H. L. Dozier (1), [USNM]; Wickham (2), [USNM].

Onthophagus antillarum Arrow

Onthophagus antillarum Arrow, 1903, Trans. Ent. Soc. London, 1903, pt. 4, p. 510; Leng and Mutchler, 1914. Bull. American Mus. Nat. His., vol. 33, p. 438; Boucomont, 1932, Ann. Soc. Ent. France, vol. 101, p. 307; Blackwelder, 1944, United States Nat. Mus. Bull. 185, p. 211; Paulian, 1947, Coléoptères des Antilles, p. 35.

Onthophagus femoralis, Fleutiaux and Sallé, 1889 (nec Kirsch, 1870), Ann. Soc. Ent. France, ser. 6, vol. 9, p. 395; Leng and Mutchler, 1914, Bull. American Mus. Nat. His., vol. 33, p. 438; Blackwelder, 1944, United States Nat. Mus. Bull. 185, p. 211.

Description. — Entirely alutaceous or sericeous. Head and pronotum from dark green to black with faint greenish reflexions, pale brown along anterolateral margins of pronotum, elytra pale brown to nearly black with lighter infusions, sometimes restricted to extreme base of elytron. Metasternum with faint pale area near midcoxal margin. Legs and antennae reddish brown, ventral surfaces of femora from yellow to light reddish brown, contrasting with darker venter. Abdominal sternites and pygidium brown with irregular lighter areas, reflexed portions of sternites yellow to yellowish brown. Head rounded, edge of clypeus rounded, cephalic punctuation and sculpturing differing in the sexes. Pronotal surface entirely punctate, the punctures denser and more impressed anteriorly and laterally. At least some anterior and lateral punctures with a short seta. Interpunctural surface very finely shagreened. A faint, shallow median longitudinal sulcus on basal half of pronotum. Pronotal sculpturing differing in the sexes. Mesosternum very coarsely and densely punctate, with a median anterior shiny spot. Anterior part of median lobe of metasternum and lateral lobes densely punctate, setigerous and shagreened, rest smooth. Elytral striae consisting of two fine parallel ridges, not deeper than interstriae, indistinctly punctate. Interstriae completely flat, entirely finely shagreened, with sparse, fine to coarse punctures bearing setae visible at least posteriorly and laterally. Epipleura densely setigerous-punctate. Abdominal sternites alutaceous, with a row of punctures bearing long setae along basal edge of each sternite. Pygidium completely margined, the disc alutaceous, finely to coarsely and fairly densely punctate, each puncture bearing a moderately long seta. Aedeagus as in fig. 7. Total length 4.5-7.5 mm.

Sexual dimorphism. — Male: Anterior edge of clypeus strongly reflexed. Clypeus with a fine, sharp, slightly arcuate transverse carina joining the two clypeo-genal sutures, which are finely carinate. From with two taurine horns

Fig. 12, Onthophagus antillarum Arrow, &.

issuing behind the eyes and curving backward and upward (fig. 12). A low but sharp, distinctly arcuate carina joining the bases of these horns across frons, not running up horns. Head entirely punctate, the punctures coarsest on genae, finest on vertex. Median pronotal prominence in form of a transverse gibbosity delimited laterally by almost impunctate anterolateral depressions (fig. 12), which receive the head horns. Last abdominal sternite greatly shortened medially. Female: Anterior edge of clypeus not strongly reflexed, normally margined, clypeal surface strongly transversely rugose. Clypeus with a strong, slightly arcuate transverse carina joining the two clypeo-genal sutures, this carina more prominent medially. Frons with a prominent, sharp transverse carina running between the eyes without reaching them. This carina straight for most of its length (fig. 2). Pronotum with transverse median anterior gibbosity equivalent to, but less developed than, that of male; without anterolateral depressions. Last abdominal sternite not shortened medially.

Type. — St. Vincent. BMNH.

Geographical variation. — There is an extreme degree of geographical variation within this species, and with a little practice it is possible to tell which island a specimen has come from in most instances. There has been no evident change in the characteristics of the Grenada and St. Vincent populations in the 75 years that separate the author's collecting from that of H. H. Smith. The populations may be distinguished as follows.

Grenada. — Pronotum and head with distinct green irridescent reflections in punctures and along edges; lateral and sometimes basal edges of pronotum with indistinct pale brown areas. Punctures of pronotum and elytra dense, moderately coarse, separated by about 3-4 diameters, each puncture bearing an erect seta. Elytra dark brown or black but with bases of intervals pale brown, pale areas more extensive on even-numbered intervals. Disc of pygidium infused with dark pigment in center. Total body length: 5.7-7.0 mm; elytral length along suture: 2.05-2.55 mm. One specimen is 4.5 mm long and entirely pale, as in the Bequia population.

Bequia and probably other Grenadines. — As above but extent of dark pigmentation is greatly reduced, such that even-numbered elytral intervals, and sometimes entire elytron and body, are pale brown. Total body length: 4.5-5.8 mm; elytral length along suture: 1.75-2.25 mm.

St. Vincent. — Black pigment has usually invaded entire dorsal surface, leaving only very small traces of pale brown. Green irridescence of head and pronotum is barely visible in strong light. In con-

trast to uniformly dark dorsal surfaces, pygidium is sometimes entirely yellow. A few specimens are as in Grenada population. The punctuation is as in the Grenada specimens. Total body length: 5.2-6.8 mm; elytral length along suture: 2.10-2.60 mm.

Martinique. — Pronotum with reduced pale areas but with strong metallic green reflections. Elytra with distinct pale markings, especially at bases. Punctures of dorsal surfaces much finer than in more southern populations and erect setae have disappeared from discal areas. Total body length: 5.5-7.5 mm; elytral length along suture: 2.05-2.75 mm.

Dominica and Guadeloupe. — Once again the black pigment has invaded the dorsal surfaces and often also the pygidial disc. Most specimens are entirely black dorsally with only the barest traces of green reflections; some show traces of the pale markings at the elytral bases. As in Martinican specimens, the punctuation is very fine and erect setae are not visible on discal surfaces (this will distinguish them from St. Vincent specimens, which are also dark). Total body length: 5.0-7.5 mm; elytral length along suture: 2.10-2.55 mm.

Remarks. — Arrow (1903) compares this species with O. marginicollis Harold of Central and South America, noting that it differs from the latter in being "less shining, . . . the striae are not punctured, and the horns of the male, although not longer, are more slender." O. marginicollis also has considerably more yellow pigment, otherwise the two species are very close. O. antillarum is also close to O. bidentatus Drapiez of northern South America. O. bidentatus differs from antillarum in the more coarsely punctate body surfaces, the punctures on the pronotum being separated by only one or two diameters and running together in transverse grooves on the pronotal gibbosity. The elytra are entirely brown and the pygidium and abdominal sternites are black, not yellowish as in antillarum. The body surfaces are less shagreened. Fleutiaux and Sallé (1889) ascribed the specimens from Guadeloupe to bidentatus Drapiez (of which femoralis Kirsch is a synonym). Paulian (1947) was the first correctly to identify these Guadalupan specimens.

Distribution. — Grenada, Grenadines, St. Vincent, Martinique, Dominica, Guadeloupe. Recorded here for the first time from the Grenadines, Martinique, and Dominica.

Ecology. — Occurs both in cow pastures and dry or moist forests

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from sea level to 2,400 ft elevation, but is more common at low altitudes. Seldom found in sandy soil, highly exposed or windswept pastures, or humid forests. This is a highly localized species, often not encountered in seemingly suitable localities, and is nowhere near as abundant as *Ateuchus illaesum* (Harold), with which it occurs on many islands. Found in fresh cow dung and donkey, sheep, pig, and human excrement. Flies principally at dusk and the early hours of the night.

Material examined. — 173 specimens, including three paratypes. The author's material is deposited in ANSP, BMNH, CNC, MNHN, GH, USNM.

GRENADA. St. George Parish: Mount Gay Estate, H. H. Smith (1), [BMNH]; Vendome, 4 mi NE of St. George's, 900 ft, 6 July 1965, E. G. Matthews (10); Grande Anse, sea level, 4 mi S of St. George's, 7 July 1965, E. G. Matthews (4); Perseverance Estate, sea level, 8 July 1965, E. G. Matthews (1); St. David Parish: Bacolet, sea level, 8 July 1965, E. G. Matthews (6); Westerhall, Sta. 140, 15 January 1936, R. E. Blackwelder (1), [USNM]; St. John Parish: 9 mi N of St. George's, Sta. 139, 13 January 1936, R. E. Blackwelder (3), [USNM]; St. Andrew Parish: Hope Estate, 500 ft, 8 July 1965, E. G. Matthews (2); 1 mi NE of Grenville, Sta. 151, 21 January 1936, R. E. Blackwelder (3), [USNM]; no further data: (1 paratype), [BMNH].

GRENADINES. BEQUIA: 13 July 1965, E. G. Matthews (15); CARRIACOU: 17 January 1936, Sta. 144, R. E. Blackwelder (6), [USNM].

ST. VINCENT. St. George Parish: Eyry Hill, 1,000 ft, 10 July 1965, E. G. Matthews (5); South end, H. H. Smith (1), [BMNH]; 2 mi N of Mesopotamia, Sta. 171, 11 February 1936, R. E. Blackwelder (4), [USNM]; Calliaqua, Sta. 168, 8 February 1936, R. E. Blackwelder (6), [USNM]; Charlotte Parish: Montreal (Mineral Springs), 1,500 ft, 10 July 1965, E. G. Matthews (17); St. Andrew Parish: Buccament River, 100 ft, 10 July 1965, E. G. Matthews (4); Sta. 176, 15 February 1936, R. E. Blackwelder (2), [USNM]; Pembroke Estate, Sta. 165, 6 February 1936, R. E. Blackwelder (5), [USNM]; St. David Parish: Troumaka, Sta. 175, 13 February 1936, R. E. Blackwelder (11), [USNM]; St. Patrick Parish: Wallilabou, 300 ft, 10 July 1965, E. G. Matthews (7); no further data: H. H.

Smith (2 paratypes), [BMNH], [MNHN].

MARTINIQUE. La Médaille (Rte. 3, Fort-de-France to Morne Rouge), 2,000 ft, 29 May 1964, E. G. Matthews (6); Colson Psychiatric Hospital, 2,000 ft, 31 May 1964, E. G. Matthews and R. Pinchon (7); 1 km N of St. Pierre, sea level, 30 May 1964, E. G. Matthews (2); Mt. Pelé, 2,400 ft, 1 June 1964, E. G. Matthews (1).

DOMINICA. St. Joseph Parish: Clarke Hall Estate, 1-400 ft, 24-28 May 1964, E. G. Matthews (34); St. George Parish: 2 mi E of Roseau, Sta. 245, 17 June 1936, R. E. Blackwelder (1), [USNM].

GUADELOUPE. Grande Terre: Gosier, sea level, 3 June 1964, E. G. Matthews (2); Basse Terre: 6 km S of Goyave, sea level, 4 June 1964, E. G. Matthews (3); no further data: Delauney (1), [MNHN].

Onthophagus batesi Howden and Cartwright

Onthophagus batesi Howden and Cartwright, 1963, Proc. United States Nat. Mus., vol. 114, p. 21.

Description. — Shiny, entirely black or with head and pronotum greenish. Legs piceous to brown, antennae vellowish brown. Head rounded with clypeus somewhat projecting anteriorly, truncate, cephalic punctuation and sculpturing differing in the sexes. Pronotal surface entirely, sparsely and finely punctate, the punctures slightly denser and more impressed anteriorly and laterally, separated by much more than their diameter. The punctures not setigerous. Interpunctural surface completely smooth, shiny, not at all alutaceous. Base without a median longitudinal sulcus. Pronotal sculpturing differing in the sexes. Meso-metasternal suture straight. Metasternum shiny between punctures, only very faintly shagreened. Elytral striae somewhat impressed, distinctly punctate, the punctures separated by two or three times their diameter. Interstriae flat, the surface smooth, shiny, densely punctate with small, shallow punctures which do not bear setae. Abdominal sternites smooth, with a row of punctures bearing long setae along basal edge of each sternite. Pygidium finely but completely margined, the disc densely and coarsely punctate, the punctures leaving a slight vertical impunctate mid-line or very indistinct ridge. Pygidial punctures bearing very short setae. Aedeagus as in fig. 8. Total length 7.5-8.5 mm.

Sexual dimorphism. — Male: Anterior edge of clypeus strongly reflexed, clypeal surface densely, evenly punctate. Clypeus with a very fine, slightly arcuate transverse carina joining the two clypeo-genal sutures, which are finely carinate. Frons with two taurine horns issuing behind the eyes and curving backwards and upward. A sharp, distinct arcuate carina joining the bases of these horns across frons and running up each horn. Frons and genae entirely densely punctate except for area behind frontal carina. Median pronotal promi-

nence in the form of a transverse, declivous gibbosity delimited laterally by moderate, finely punctate anterolateral depressions, which receive the head horns. End of fore tibiae with a flat triangular tooth projecting over base of fore spur. Last abdominal sternite greatly shortened medially. Fore legs only slightly slenderer than those of female. Female: Anterior edge of clypeus not reflexed, clypeal surface strongly transversely rugose before transverse clypeal carina, which is strong and merges with clypeo-genal carinae to form a single sinuate transverse carina. Frons with a prominent shelf-like transverse carina, curved backward at the edges, running between eyes. Frontal surface sparsely punctate behind this carina, densely punctate before it. Pronotum with a transverse median anterior gibbosity, less developed than that of male but laterally delimited by rather deep depressions. Terminal edge of fore tibiae without a flat projection over base of fore spur. Last abdominal sternite not shortened medially.

Type. — La Unión, El Salvador. USNM 65681.

Remarks. — A widespread species throughout Central America and lowland Mexico, this species was confused with O. incensus Say until recently. Its presence in Martinique is undoubtedly due, like that of O. bituberculatus, to artificial introduction. It is curious that the only two introduced species of Scarabaeinae in the Antilles should both be in Martinique, as they are of very different origins. From the native O. antillarum, this species may be told at a glance by its shiny surfaces and larger size. The determination of the Martinican specimens was checked by O. L. Cartwright.

Ecology. — O. batesi was collected by the author in only one spot in Martinique, a small plot of cleared sloping land behind the Psychiatric Hospital at Colson, where some cows and pigs are kept. This is a moist area at approximately 2,000 ft elevation and is similar to many other spots on the island. Undoubtedly, more collecting will reveal additional populations of this species in Martinique. The collection of Father R. Pinchon contains two specimens from Fort-de-France.

Distribution. — From Panama north through Central America and tropical Mexico to extreme southern Texas, and Martinique. Here recorded for the first time from the Antilles.

Material examined. — 9 specimens. The author's material is deposited in BMNH, CNC, MNHN, USNM.

MARTINIQUE. Colson Psychiatric Hospital, 2,000 ft, 30 and 31 May 1964, E. G. Matthews and R. Pinchon (7); Fort-de-France, 15 June and 5 July 1954, R. Pinchon (2), [RP].

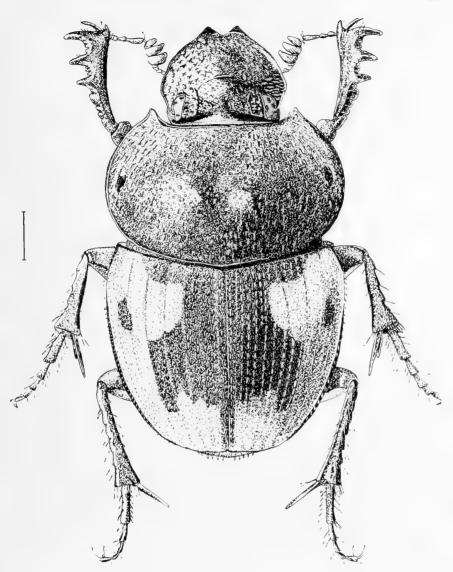


Fig. 13, Onthophagus bituberculatus (Olivier), &.

Onthophagus bituberculatus (Olivier)

Scarabaeus bituberculatus Olivier, 1789, Entomologie, vol. 1, gen. 3, p. 131, tab. 22, fig. 197.

Description. — Somewhat flattened, densely punctate and entirely covered with short, stout bristles. Body and legs piceous to black, antennal clubs yel-

low, elytra yellow with a symmetrical black pattern. Clypeus with two prominent triangular teeth separated by a V-shaped emargination. Head surface densely punctate, each puncture accompanied by a small transverse ridge and bearing a short stout seta. A small, low transverse ridge in middle of head in both sexes, head otherwise devoid of carinae or horns. Eyes large. Pronotum with lateral edges rounded, evenly curved when seen from above (fig. 13). Anterior angles prominently acute. Surface entirely very densely punctate, the punctures large, shallow, and circular, each bearing a very stout yellow seta, the setae longer laterally. These punctures interspersed with smaller simple punctures. Interpunctural surface smooth. No median longitudinal sulcus. Pronotal sculpturing differing in the sexes. Underside of prothorax without any oblique carina running laterally from front coxal cavities to lateral Median lobe of metasternum without any median gibbosity. sternum entirely sparsely punctate, the punctures bearing short stout setae. Elytral striae not impressed, with a close-set row of shallow circular punctures, the punctures separated by a distance equal to their diameter. Intervals 2-7 with three rows basally and two rows distally of regularly spaced, short stout yellow setae. First interval with one row and eighth with many rows. Elytra with a symmetrical black and yellow pattern as illustrated in fig. 13. Epipleura black, with one or two rows of setigerous punctures. Fore tibiae tridentate, but a fourth proximal tooth is indicated by a low lobe, the three distal teeth very long. Margin between teeth strongly serrate. Fore spur linear, curved downward. Ventral surface of middle and hind femora with two or three rows of well-separated, long setae. Hind tibiae very slender, straight, not strongly expanded distally. Hind metatarsus distinctly shorter than remaining tarsal segments combined. Abdominal sternites smooth, with a close-set row of shallow punctures along the base of each sternite, additional punctures laterally on fourth and fifth sternite. Disc of pygidium almost flat, very densely punctate with shallow, circular, setigerous punctures. Aedeagus with parameres rounded (fig. 9). Total length 6.5-9 mm.

Sexual dimorphism. — Male: Head proportionately a little longer than that of female, the clypeal teeth not so prominent. Pronotum with two approximated, low conical gibbosities on either side of mid-line a little behind middle of pronotal area. Fore tibiae with the inner distal angle drawn out into a spurlike process which is downwardly curved and shorter than the fore spur. Last abdominal sternite somewhat shortened medially. Pygidium only a little wider than long. Female: Head proportionately a little shorter but with the clypeal teeth more prominent and reflexed. Pronotum without any gibbosities. Fore tibiae with the inner distal angle not drawn out into a process. Last abdominal sternite greatly elongated, the pygidium much wider than long.

Type. — Senegal. MNHN.

Remarks. — This species belongs in d'Orbigny's (1913) 32nd group of African Onthophagus. A specimen from Dakar, Senegal, compared with the type by Dr. Descarpentries, was sent from the

Paris Museum and compared with the Martinican specimens by the present author. No differences could be observed. It is curious that the only other known African *Onthophagus* introduced into the New World, *O. depressus* Harold, should also belong to the 32nd group. It was discovered in Georgia by P. W. Fattig and reported by Cartwright (1938) and now also occurs in Florida. The two species are very similar in appearance, but may be told apart immediately by the absence of the yellow elytral pattern in *depressus*.

Ecology. — O. bituberculatus was found in only two localities in Martinique, both north of St. Pierre. Most specimens were dug out from under cow manure and straw in a deep sand plot on the sea's edge at the northern outskirts of the town. The others were in a very dry pasture on the low lava slopes in the rain shadow of Mt. Pelé, a few kilometers to the north. Evidently, dry, sandy pastures are preferred by this species.

Distribution. — West Africa from the Congo to Senegal, the Sudan, Egypt, and part of Arabia (d'Orbigny, 1913). Martinique. Recorded here for the first time from the Western Hemisphere.

Material examined. — 10 specimens, including one from Dakar, Senegal, determined by Boucomont and compared with the type by Descarpentries. The author's material is deposited in BMNH, CNC, MNHN, USNM.

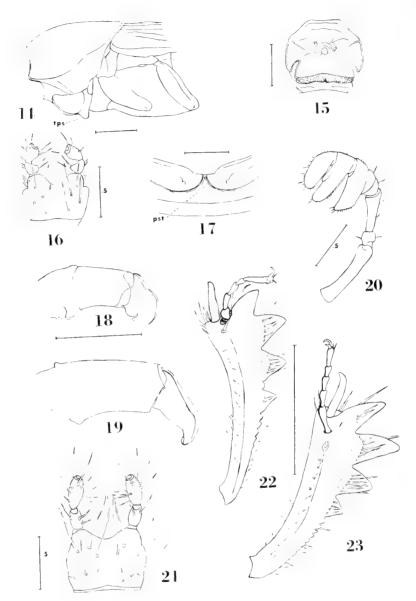
MARTINIQUE. 1 and 5 km N of St. Pierre, sea level, 30 May 1964, E. G. Matthews (9).

Genus ONITICELLUS Serville

Oniticellus Serville, 1825, Encyclopédie méthodique, Entomologie vol. 10, p. 356.

Type of genus. - Scarabaeus cinctus Fabricius, 1775.

Description. — Oblong, yellowish brown to dark brown, seldom black, pilosity when present never bristly, squamose, exceptionally very long. Head entirely unarmed (Oniticellus s. str.) or with one to three transverse carinae (most species of Euoniticellus Janssens), seldom with a tubercle or horn. Genal margins either rounded, forming a continuous line with clypeus, or feebly bent in at clypeo-genal junction (Oniticellus s. str.), or strongly bent out here, continuing backward as parallel edges, there being a strong emargination at clypeo-genal suture (Euoniticellus). Pronotum always unarmed, the base nearly always unmargined. Elytra feebly convex, sometimes flat. Scutellum visible. Apical edges of elytra with a dense row of long, projecting, more



Figures 14-23. Fig. 14, Oniticellus cubiensis Laporte, \$\partial \text{, lateral view of thorax: tps} — tumescence of prosternum. Fig. 15, Oniticellus cubiensis Laporte, \$\partial \text{, head.}\$ Fig. 16, Oniticellus cubiensis Laporte, labium. Fig. 17, Oniticellus cubiensis Laporte, part of hind coxae and first two abdominal sternites; pst — process of first sternite between hind coxae. Fig. 18, Oniticellus cubiensis Laporte, aedeagus. Fig. 19, Drepanocerus reconditus n. sp., aedeagus.

or less stiff hairs. Seldom is the row of hairs so shortened that it persists only in the region of sutural angle, in which case it still runs in a transverse, never a longitudinal, direction. Exceptionally apical fringe is tufted. Pygidium basally unmargined. In subgenus *Euoniticellus* apical half nearly always has a dark, shiny spot. Prosternum behind fore coxae, especially in males, with a trapezoid gibbosity or a more or less developed process. First sternite forming a more or less acute process between hind coxae (fig. 17, pst), which are somewhat more separated in *Euoniticellus* than in *Oniticellus*.

Distribution. — Ethiopian Region (14 species), Palaearctic (4), Oriental (3). One species in the Western Hemisphere, restricted to Jamaica, Cuba, and the Bahamas. Recorded here for the first time from the Bahamas.

Remarks. — A genus of Ethiopian origin, Oniticellus probably entered North America from Asia via the Bering Bridge. It now shows a relict distribution in the New World, being extinct on the continent (continental species sometimes ascribed to Oniticellus belong to the genus Liatongus).

Janssens (1953), in his revision of the world Oniticellini, divided the present genus into two separate ones: Oniticellus Serville and Euoniticellus Janssens. O. cubiensis Laporte was placed in Euoniticellus, but in his key to species Janssens immediately separated O. cubiensis in the first couplet for not possessing projecting genal margins — one of the key features of his genus Euoniticellus. Evidently O. cubiensis occupies an isolated position and does not fit properly into either of Janssens' categories. Principally for this reason, the author agrees with Balthasar (1963) in reuniting Oniticellus and Euoniticellus as a single genus. Balthasar (from whom the above generic description is taken) maintains Janssens' categories as subgenera, but O. cubiensis should perhaps occupy a subgenus of its own, if the subgeneric categories are to be maintained.

Oniticellus cubiensis Laporte de Castelnau

Oniticellus cubiensis Laporte, 1840, Histoire naturelle des animaux articulés, vol. 2, p. 92; Chevrolat, 1864, Ann. Soc. Ent. France, ser. 4, vol. 4, p. 410; Leng and Mutchler, 1914, Bull. American Mus. Nat. His., vol. 33, p. 438; Gowdey, 1926, Catalogus insectorum jamaicensis, p. 18.

Fig. 20, Drepanocerus reconditus n. sp., antenna. Fig. 21, Drepanocerus reconditus n. sp., labium. Fig. 22, Drepanocerus reconditus n. sp., 3, underside of left fore tibia. Fig. 23, Drepanocerus reconditus n. sp., 4, underside of left fore tibia.

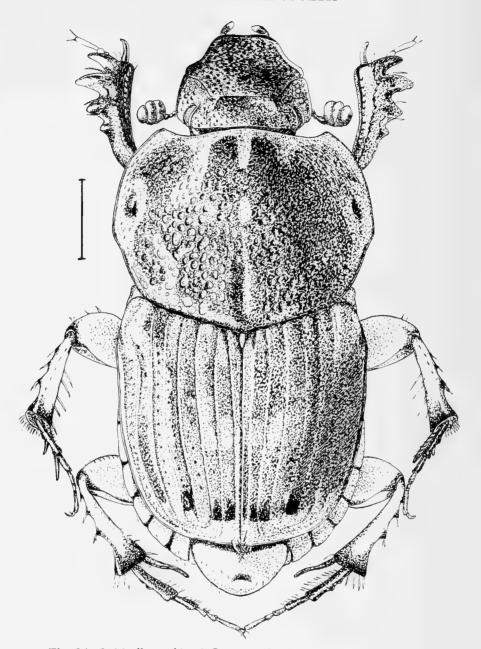


Fig. 24, Oniticellus cubiensis Laporte, 9.

Description. — Dull, light brown in color with extensive dark brown markings over all surfaces, dorsally arranged in the pattern represented in fig. 24. Some distinct cupreous reflections on head and pronotum. Forelegs fuscous, remaining legs lighter, yellow, with fuscous markings. Antennae dark. Pygidium with a central dark spot. Clypeus not dentate or emarginate, widening in a curve basally, the edge slightly projecting beyond that of genae just before clypeo-genal suture. Edges of genae not parallel, diverging basally. Head entirely strongly margined, occipital carina strong and complete, head surface strongly rugose and punctate, more finely punctate and shagreened on vertex behind ridge or horn. Eves small, Antennae eight-segmented, the second segment globular, the third longer than remaining segments. Labium with lateral margin excised distally, labial palpi with first segment triangular, second segment expanding distally, larger, third segment extremely minute (fig. 16). Line delimiting gula and submentum straight. Pronotum slightly rhomboidal, very slightly wider at widest point than elytra, anterior angles rounded, lateral angles approximately medial, posterior angles very broadly rounded. Base of pronotum not margined. Pronotal surface very densely and coarsely punctate with punctures of two sizes, the surface also very finely shagreened. Median longitudinal sulcus basal, rather deeply impressed. Propleurae with a carina emerging from anterior coxal cavities and extending obliquely toward lateral edge of prothorax, without reaching it. Prosternum with a laminate projection between coxae, and with a tumescence behind coxae in female, this tumescence reduced to a shiny flat surface in male. Mesosternum densely rugulose, matt, except for a shiny median longitudinal carina. Meso-metasternal suture straight except for a small acute median posterior projection. Metasternum finely and sparsely punctate, with tortoise-shell markings. Configuration of episterna and epimera as in fig. 14, metepisternal edge strongly sinuate posteriorly. Elytra leaving edges of abdominal sternites uncovered laterally. Eight striae, including one along epipleuron, shallow, indistinctly punctate. Elytra glabrous except for a few long setae emerging in an irregular row from first interstria very near posterior apex, which is without a marginal fringe of setae. Epipleura narrow, vertical. Scutellum small but distinct, elongate, medially grooved. Fore tibiae with four broad, rounded outer teeth, the proximal one small, the apical one directed obliquely forward, with a large, straight movable spur and long tarsus. Femora very finely punctate. Middle and hind tibiae abruptly expanding apically, with three short transverse carinae. Middle and hind tarsi a little longer than tibiae, the first segment of hind tarsi sublinear, only slightly shorter than remaining segments combined, which are subtriangular. Tarsal claws simple, small. Six visible abdominal sternites shagreened, with a row of coarse, evenly spaced bristles along anterior edge of each sternite. Pygidium without a trace of a margin or carina across base, outer edges finely margined. Pygidial surface sparsely punctate, each puncture with a long seta. Center of disc with a smooth, shiny dark area contrasting with the yellow matt of disc. Aedeagus as in fig. 18, with the parameres very short, rounded, and ventrally excised. Total length 6.5-7.5 mm.

Sexual dimorphism. — Male: Head with a short, stout horn on middle of vertex, with a transverse ridge across middle of clypeus, followed by a pair of curved ridges running on clypeus between clypeo-genal angles and horn (fig. 15). Pronotum gibbous anteriorly. Fore tarsus with first segment globular, inserted near base of fore spur. Prosternum behind fore coxae only slightly tumescent, flattened and shiny medially. Last abdominal sternite shortened medially, pygidium as long as wide. Female: Head without clypeal ridges or horn, with only one wide, straight, transverse clypeo-frontal carina (fig. 24). Pronotum not gibbous anteriorly. Fore tarsi with first segment long, linear, inserted well away from spur. Prosternum behind front coxae with a prominent median tumescence (fig. 14, tps). Last abdominal sternite not shortened medially, pygidium wider than long.

Type. — Cuba. Not found in MNHN.

Remarks. — At first glance this appears to be a typical Oniticellus of the subgenus Euoniticellus Janssens, but a number of features sets it apart. The shape of the head, the presence of a head horn in the male, the prosternal tumescence being confined to the female, and especially the absence of a distinct transverse row of long hairs on the distal edges of the elytra, are all features rare or absent in other members of the genus. Its taxonomic isolation indicates that it could not be an introduced species in the Antilles, in spite of its very successful adaptation to the culture-steppe.

O. cubiensis is the only scarabaeine species in the Greater Antilles which occurs on more than one island, and the apparent absence of any geographical variation suggests that it recently jumped from one island to the others. We have no clue as to whether it is originally from Cuba or Jamaica; the presence of another relict oniticelline species in Jamaica (Drepanocerus reconditus n. sp.) vaguely points to this island as the original home.

Ecology. — This is the only species collected by the author in the Antillean region which apparently never enters forests. Even traps set near the edges of wooded areas in Jamaica (but inside them) do not collect any O. cubiensis. On the other hand, it is very successfully adapted to open terrain, such as roadsides and pastures, and it often exploits cow dung intensively. In Jamaica it was found in every type of open terrain at all altitudes up to 2,400 ft, but more abundantly near sea level. No edaphic preferences were noted.

Distribution. — Jamaica, Cuba, Isle of Pines, Bahamas. Recorded here for the first time from the Bahamas. It is repeatedly

cited from Florida in United States catalogues and lists, but this record is based on a note in a manuscript by Schwarz cited by Blatchley (1928), and possibly based on an accidental specimen. Recent searching has failed to reveal the presence of *O. cubiensis* in Florida (R. E. Woodruff, *in litt*.) and there is no reason to continue citing it from there.

Material examined. — 151 specimens. The author's material is deposited in ANSP, BMNH, and MNHN.

JAMAICA. St. Thomas Parish: Bath Fountain, 150 ft, 18 July 1961 (1), [SMIJ]; Morant Bay Rd., sea level, 28, 31 March 1964 (2), [SMIJ]; Booby South Point, sea level, 30 July 1965, E. G. Matthews (5); St. Andrew Parish: Ferry, 100 ft, 7 October 1946, G. B. Thompson (5), [SMIJ]; Kingston, sea level, 2-3 July 1935, B. and C. (2), [SMIJ]; 7½ mi E of Kingston, sea level, 9 October 1964, E. G. Matthews (19); Kingston, Sta. 1, 1 July 1935, R. E. Blackwelder (10), [USNM]; 29 January 1937 (6), [USNM]; Portland Parish: Durham, 170 ft, 7 August 1947, G. B. Thompson (1), [SMIJ]; E of Buff Bay, sea level, 28 July 1965, E. G. Matthews (1); Green Hill — Wakefield, mi 28-29, 2,400 ft, 28 July 1965, E. G. Matthews (2); W of Port Antonio, sea level, 28 July 1965, E. G. Matthews (3); 3.5 mi E of Port Antonio, sea level, 28 July 1965, E. G. Matthews (2); Rd. to Ecclesdown, 600 ft, 28 July 1965, E. G. Matthews (3); Hope Bay, Sta. 363, 30 January 1937, R. E. Blackwelder (1), [USNM]; St. Catherine Parish: Jamaica School of Agriculture, 11 mi W of Kingston, sea level, 29 January 1964 (1), [SMIJ]; Manchester Parish: Agriculture Ministry Farm, Grove Place, 1,500 ft, 11 October 1964, E. G. Matthews and T. H. Farr (2); 4 mi SE of Balaclava, Sta. 397, 13 February 1937, Chapin and Blackwelder (20), [USNM]; Oxford R., Sta. 399, 14 February 1937, Chapin and Blackwelder (11), [USNM]; St. Ann's Parish: St. Ann, January 1917, A. H. Ritchie (1), [BMNH]; 5 mi S of Moneague, Sta. 12, 18 July 1935, R. E. Blackwelder (2), [USNM]; Clarendon Parish: May Pen, Sta. 425, 28 February 1937, Chapin and Blackwelder (3), [USNM]; St. Elizabeth Parish: Quickstep, 1,500 ft, 10 August 1941, C. B. Lewis (1), [SMIJ]; Braes River — Elim, 500 ft, 31 July 1965, E. G. Matthews (2); Black River, sea level, 24 February 1937, B. and C. (2), [SMIJ]; mi 13, Black River — Malvern Rd., 2,000 ft, 31 July 1965, E. G. Matthews (2); Black River, Sta. 419, 24 February 1937, Chapin and Blackwelder (11), [USNM]; *Trelawny Parish:* Hampden-Wakefield, 500 ft, 2 August 1965, E. G. Matthews (1); *St. James Parish:* N of Niagara, 1,500 ft, 31 July 1965, E. G. Matthews (2); Montego Bay, 15 March 1911 (1), [USNM]; *Westmoreland Parish:* Pondicherry, 2,200 ft, 2 August 1965, E. G. Matthews (1); Darliston, December 1917, A. H. Ritchie (1), [USNM]; *no further data:* (8), [BMNH].

CUBA. *Pinar del Río:* San Vicente, R. E. Woodruff, 16 August 1959 (7), [GH]; *Camagüey:* Camagüey, 20 August 1924, J. Acuña (2), [USNM]; *Oriente:* Santiago, sea level, November 1947, Alayo (1), [FZ]; *no further data:* (2), [BMNH]; Ex Musaeo Harold (1), [MNHN].

BAHAMAS. New Providence: Nassau, Fred. K. Knab (1), [USNM]; ELEUTHERA: New Portsmouth (Rock Sound), 28 March 1953, E. B. Hayden, Van Voast-AMNH Bahama Isl. Exped. (2), [USNM].

Genus DREPANOCERUS Kirby

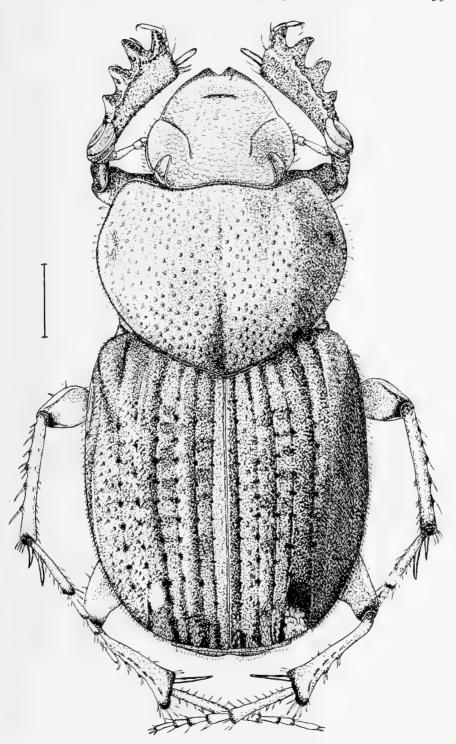
Drepanocerus Kirby, 1828, Zool. J., Vol. 3, p. 521.

Type of genus. - Drepanocerus kirbyi Kirby, 1828.

Description. — Oblong, dorsal surface generally depressed, rugose and opaque, with strong sculpturing, provided in part with stout bristles or thick squamae, more or less densely distributed. Clypeus nearly always emarginate anteriorly, rarely truncate or entire, usually forming a sinus or angular emargination where it joins genae. Pronotum normally with depressions, more or less developed, often limited by carinae which may form cell-like partitions. Scutellum sometimes indistinct and sunken between internal angles of elytra, often clearly visible, in which case the edges rest over margins of suture. Elytra subplanate, often ornamented with ridges, usually showing small carinae on humeral callus and tufts of more or less squamiform setae on apical declivities. Eighth interstria not or barely wider than seventh. Epipleura absent or quite narrow. Pygidium with a transverse margin or carina on base, often ornamented with tubercles or carinae. Posterior coxae not contiguous. Fore tibiae sometimes very elongated and bent inward, head and pronotum sometimes armed with horns in males. Tarsi generally fairly long and slender.

Distribution. — Ethiopian Region (18 species), Oriental Region (9 species, of which two enter China). One species in the Western

Fig. 25, Drepanocerus reconditus n. sp., &, holotype.



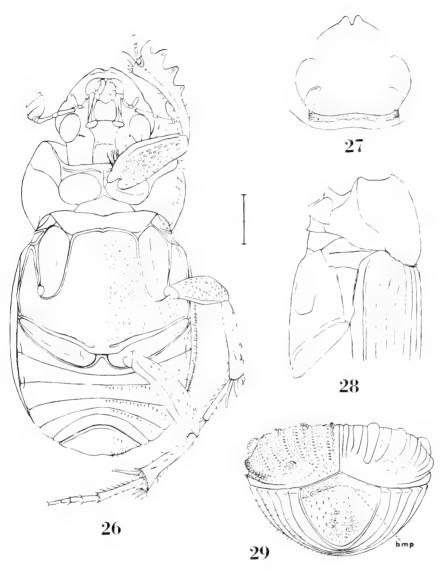
MEM. AMER. ENT. SOC., 21

Hemisphere, restricted to Jamaica. This genus is here recorded for the first time from the Western Hemisphere.

Remarks. — The origin and dispersal of this genus are the same as those mentioned for *Oniticellus*, and the two genera evidently have had the same history in the Western Hemisphere. Both are represented by a single relict species in Jamaica which is taxonomically isolated within its respective genus.

Drepanocerus reconditus n. sp.

Description. - Dark brown, entirely tomentose and opaque above, legs luteous with darker areas (fig. 25). Entirely devoid of projections, sharp carinae, or depressions. Elytra broader than pronotum, which is feebly developed. Head subtriangular, the clypeus medially emarginate and bidentate, margin at junction of clypeus and genae not angulate or very obtusely so, genae not appreciably projecting, obtusely rounded. Entire head surface very densely covered with large, shallow punctures, the surface inside the punctures finely granulate, each puncture bearing a very short seta. Dorsal areas of eyes small. Occiput margined by a sharp declivity, followed by a transverse, opaque depression (fig. 27). Antennae eight-segmented, the third segment long (fig. 20), labium subquadrate with a rounded anterior emargination, labial palpi with second segment larger than first, third segment represented by a small tubercle at end of second segment (fig. 21). Pronotum somewhat cordate, the anterior angles acutely rounded, the lateral and hind edges forming an even arc, slightly angulate at middle of base (fig. 5). Base not margined, lateral margin terminating opposite humeri. Entire pronotal surface densely and evenly covered with short, stout setae, surface between setae distinctly shagreened. Median longitudinal depression more impressed basally, otherwise pronotum entirely devoid of carinae or impressions. Propleura with oblique carina (fig. 26), but not excavated anteriorly. Sterna with configurations illustrated in figs. 26 and 28. Prosternum without any carinae, explanations, or tumescences, other than a moderate median longitudinal ridge between coxae. Mesometasternal suture straight, metasternal surface coarsely, densely, and evenly punctate except on midline, interpunctural surface shagreened. Middle coxal cavities widely separated. Metepisternum elongate, with shape shown in fig. 28. Elytra with eight striae, each stria impressed and bearing a row of large punctures. Interstriae convex, with somewhat uneven, shagreened surface, and entirely densely covered with very short stout setae, tending to be squamiform and to concentrate on humeral and apical calli. A darker, glabrous area just before apical callus of fifth interval. Intervals 3 and 5 more raised than others, intervals 6 and 7 somewhat depressed behind prominent humeral callus. Elytra not fringed with long setae posteriorly, covering entire abdomen along the sides, such that sternites are not visible from above. Epipleura narrow, vertical. Scutellum sunken, small, normally covered by hind edge of pronotum. Fore tibiae with four outer teeth,



Figures 26-29. Fig. 26, Drepanocerus reconditus n. sp., δ , ventral view. Fig. 27, Drepanocerus reconditus n. sp., β , head. Fig. 28, Drepanocerus reconditus n. sp., δ , lateral view of thorax. Fig. 29, Drepanocerus reconditus n. sp., δ , posterior view of body; setae are shown on left side only: bmp—basal margin of pygidium.

the apical one directed obliquely forward, with a large movable spur and long tarsi (figs. 22, 23). Middle and hind femora densely punctate, the tibiae expanding abruptly apically, with seta-tufts but no transverse carinae. Middle and hind tarsi equal in length to tibiae. First tarsal segment, which is sublinear, slightly shorter than remaining segments combined, which are subtriangular. Claws simple, moderate. Six visible abdominal sternites with matt, shagreened surface and each with a transverse row of large setigerous punctures. Pygidium not distinctly carinate basally, but with a line of short setae delimiting a smoother basal margin (fig. 29, bmp). Pygidial disc with coarse, close-set setigerous punctures. Interpunctural surface shagreened. Disc devoid of projections or shiny spots, but with a low tumescence on either side of midline. Aedeagus as in fig. 19. Total length 7.5-9.0 mm.

Sexual dimorphism. — Male: With clypeal emargination and teeth angular (fig. 25), fore tibiae slightly more slender than those of female, with first tarsal segment short and globular, inserted near spur (fig. 22), last abdominal sternite shorter than penultimate one, and pygidium longer than wide (fig. 29). Female: With clypeal emargination and teeth rounded (fig. 27), fore tibiae stouter, first tarsal segment very long and inserted well away from spur (fig. 23), last abdominal sternite subequal in length to penultimate, and pygidium wider than long.

Type. — Hardwar Gap, Jamaica. USNM.

Remarks. — This species fits Janssens' (1953) description of the genus Drepanocerus (quoted above) fairly well, but it shows a number of unusual features, as follows. The body surface is not strongly sculptured with ridges and depressions as in most species, and there are no carinae on the humeri. The species is unusually large for a Drepanocerus, particularly as the forms without a visible scutellum are normally the smallest ones (Janssens, op. cit.), and there is an extreme reduction in the degree of sexual dimorphism. The middle and hind tibiae abruptly enlarge distally, as in Oniticellus cubiensis, whereas in the Old World Drepanocerus examined these enlarge gradually. However, many essential features, such as the dense stout setae, emarginate clypeus, sunken scutellum, basal pygidial margin, and separated hind coxae, are those of Drepanocerus and there is no other existing oniticelline genus in which D. reconditus could possibly fit. In all available keys to Old World oniticelline genera (e.g. Balthasar, 1963), this species goes directly to the genus Drepanocerus without difficulty.

In Janssens' (1953) key to the world species of the genus, D. reconditus does not fit even the first couplet and any attempt to force it through to a possible close relative meets with failure. Evidently

this is a highly isolated species within the genus.

Ecology. — The area in which this species is found is covered with moderately dense moist forest. The rainfall in the region is around 90 inches a year (Taylor, 1956) and so it is by no means one of the wettest parts of the island. It is, however, the highest point which can be reached by road (4,300 ft) and evidently altitude is the crucial factor involved in the distribution of the species. In spite of general trapping throughout the area, both along the road on both sides of the Blue Mountain ridge and along footpaths, this species was found only in an area not over 200 meters wide well inside the forest, both in October, 1964, and July, 1965. This extremely restricted distribution suggests that we are dealing with a marginal population and that the main range of the species will be found to be higher up or further inside the undisturbed forests of the Blue Mountains, which climb to over 7,000 ft.

D. reconditus comes to human, cow, and an unidentified black excrement (feral cat?), and two specimens were collected with a dead lizard as bait, indicating necrophagous tendencies. The largest number of specimens (16) was collected in the morning under human excrement deposited on a footpath. This same excrement had been inspected by the writer the afternoon previously, when it had already been lying for some time, without yielding any specimens. This fact indicates that the Drepanocerus arrived during the night and that the species is therefore nocturnal. Furthermore, not a trace of any excavation could be seen under the excrement, suggesting that this species does not dig. Its feeble physical development points to the same conclusion.

The biology of the world *Drepanocerus* is almost totally unknown, but remarks by Janssens (1953) indicate that the African species are also forest inhabiting and do not excavate.

Distribution. — Jamaica (fig. 129).

Material examined. — 28 specimens. Paratypes are deposited in BMNH, CNC, GH, MNHN, SMIJ, USNM.

JAMAICA. *Portland Parish:* Hardwar Gap, N side, 4,300 ft, 9 October 1964, E. G. Matthews and T. H. Farr (7); 28 July 1965, E. G. Matthews (21).

Genus PHANAEUS MacLeay

Phanaeus MacLeay, 1819, Horae entomologicae, vol. 1, pt. 1, p. 124.

Type of genus. — Phanaeus vindex MacLeay, 1819.

Description. - Large, powerful beetles, often brilliantly colored and ornamented with horns or carinae on head and pronotum of both sexes. Head broadly semicircular. Antennae nine-segmented, the last two segments of antennal club partly enclosed in enlarged, cup-like first segment. Labium deeply emarginate, palpi with first segment very large, broad, second segment smaller, elongate, third segment small, cylindrical, glabrous. Propleurae not bearing an oblique transverse carina, not anteriorly excavated. Hind edge of pronotum margined, medially angulate but not forming an acute median projection. Mesosternum extremely short, hidden. Median lobe of metasternum forming a forwardly directed angular gibbosity which, however, is never drawn out into a long process. Scutellum absent. Elytra with eight striae, nearly always distinct, epipleura very narrow, vertical. Legs strong, fore tibiae slender with three outer teeth rounded, not prominent. Hind tibiae usually without transverse carinae on outer face. Front tarsi absent in male, usually present in female. All tarsi with five segments, without claws. Abdominal sternites not fused or strongly narrowed medially, sixth sternite nearly vertical, pygidium small, semicircular, fully margined.

Distribution. — Neotropical Region (\pm 100 species), Nearctic (9). One species in the Antilles, restricted to Jamaica.

Remarks. — A genus of South American origin, *Phanaeus* shows extensive penetration of Central and North America, which it must have invaded early (in the Upper Cretaceous or Eocene, according to Halffter, 1964).

Olsoufieff (1924), in what continues to be the only definitive revision of the genus, divided *Phanaeus* into five subgenera, one of which (*Sulcophanaeus* Olsoufieff) contains *Ph. carnifex* (Linnaeus) and a Colombian species, *Ph. steinheili* Harold. The basis of the subgenus is the form of the male genitalia and the absence of front tarsi in both sexes. However, Olsoufieff was rather uncertain about the affinities of these two species, and was inclined to consider *carnifex* (under the name *sulcatus* Drury) as completely isolated within the genus. This taxonomic isolation suggests that *carnifex* reached Jamaica a long time ago.



Fig. 30, Phanaeus carnifex (Linnaeus), 8.

Phanaeus carnifex (Linnaeus)

Scarabaeus carnifex Linnaeus, 1758, Systema naturae, ed. 10, vol. 1, p. 346. Phanaeus carnifex (Linnaeus), Barber, 1928, J. Acad. Sci. Washington, vol. 18, p. 383; Pereira and Martínez, 1956, Rev. brasileira Ent., vol. 5, p. 229; Landin, 1956, Ent. Tidskrift, vol. 77, pt. 1, p. 3.

Scarabaeus sulcatus Drury, 1770, Illustrations of natural history, vol. 1, p. 76. Phanaeus sulcatus (Drury), Leng and Mutchler, 1914, Bull. American Mus. Nat. His., vol. 33, p. 438; Olsoufieff, 1924, Insecta, Rennes, vol. 13, p. 78; Gowdey, 1926, Catalogus insectorum jamaicensis, p. 18.

Scarabaeus sphinx Fabricius, 1772, Ent. Syst. vol. 1, p. 25.

Scarabaeus belzebul Fabricius, 1775, Systema entomologiae, p. 23.

Scarabaeus nicanor Fabricius, 1781, Species insectorum, vol. 1, p. 27. Scarabaeus lar Herbst, 1789, Natursystem, Käfer, vol. 2, p. 48. Phanaeus moloch MacLeay, 1819, Horae entomologicae, vol. 1, pt. 1. p. 129.

Description. — Entirely slate-black, the antennal clubs rufous. Clypeal margin feebly bidentate in both sexes. Head surface densely transversely rugose, anterior surface of horn densely punctate. Lower margin of hind angles of genae projecting backward beyond carinate upper margin. oblique carina in front of and paralleling anterolateral edge of eye. See figs. 30 and 32 for head sculpturing in both sexes. Anterior angles of pronotum prominent, lateral margin angled out at origin of lateral carina. Lateral carina prominent, sharp and long in both sexes (figs, 30 and 32). Base of pronotum with two short, very deep longitudinal furrows emerging from margin on either side of middle. Median longitudinal groove sharp, impressed on disc anterior to these furrows. Pronotal disc finely and densely punctate in male, coarsely aspero-punctate in female. Anterior declivities smooth, shiny, complexly sculptured. See figs. 30 and 32 for pronotal sculpturing in both sexes. Median anterior prominence of metasternum densely and very finely punctate, the median longitudinal groove deeply impressed posteriorly. Sloping portions of metasternum and pleural sclerites very densely punctate and pilose. Elytral striae feeble, impunctate, striae 2-5 emerging from very deep basal pits. Interstriae with feebly convex, rounded median longitudinal ridges. Elytral surface very finely punctate, smooth and sericeous. Sutural margin splayed out for basal third, forming long narrow pseudo-scutellum. Anterior tibiae slender, obtusely tridentate, with long spur but devoid of tarsi in both sexes. Middle femora with ventral surface very densely pilose on distal half. Middle tibiae very strongly expanded distally, the tarsal segments very short and wide. Hind femora with a few pilose punctures distally on ventral surface. Hind tibiae very pilose, with a strong transverse carina on outer face subdistally, strongly expanded distally. Tarsal segments very wide. Abdominal sternites smooth, each with a row of setigerous punctures along base laterally. Pygidium small, somewhat semicircular, the basal margin strongly curved toward disc medially. Disc smooth, very finely punctate. Aedeagus as in fig. 33. Total length 17-25 mm.

Type. — Jamaica. Lost.

Remarks. — Considerable confusion continues to attend the designation of the name carnifex Linnaeus. It seems obvious that Linnaeus originally (in 1758) intended to apply the name to the Jamaican species of *Phanaeus*, as he gives Jamaica as the habitat and refers to one illustration (that of Brown, 1756) which is unmistakably of the Jamaican species (R. D. Pope, in litt.). Unfortunately, his accompanying description is useless. Contrary to what Barber (1928) states, Linnaeus did base his description on at least one specimen,

since he followed all descriptions based only on literary evidence with a dagger (†), not present in this case. The confusion arose first when Linnaeus himself mis-applied the name carnifex to two continental species in 1767, one of which (Phanaeus vindex MacLeay) continued to bear the name in literature until recently. The problem has been further compounded by the loss of the original type or series. The Linnaen collection in London contains four specimens under the name carnifex, but none of these is the Jamaican species (R. D. Pope, in litt.), contrary to what Landin (1956) implies when he refers to these specimens as "Phanaeus carnifex auct." The Linnaen collection in Uppsala does not contain any specimens under the name carnifex (Landin, op. cit.).

The only way to preserve the present usage of the name *carnifex* Linnaeus, as applied to the Jamaican species, is to hereby designate the figure in Brown (1756, pt. III, book III, chapt. I, class II, sect. III, art. I, second figure of 5 *Scarabaeus*), which is unmistakably of the Jamaican species, as lectotype of *Scarabaeus carnifex* Linnaeus, 1758. Since this figure is cited by Linnaeus (as Brown jam. 428. t. 43f. 5. Scarabaeus cornu incurvo) it may be considered as part of the type series.

As pointed out by Olsoufieff (1924), *Ph. carnifex* is taxonomically isolated within the genus by the form of the male genitalia, male pronotal ornamentation, and the absence of fore tarsi in both sexes. Additional features which seem unusual to the present author (who has not examined all the species of the genus) are the all-black color, normal only among the nocturnal and necrophagous species of the subgenus *Coprophanaeus*, the arrangement of carinae at the hind angles of the head, the prominent lateral carina of the pronotum and its two deep basal impressions, the splayed-out elytral sutural margin, the strong transverse carina on the hind tibiae, and the strongly curved basal pygidial margin.

Ecology. — This species is diurnal, coprophagous, and well adapted to open terrain, although it may be trapped in numbers in forests as well. Its upper altitude limit appears to be 2,200 ft, but there is evidence that altitude factors alone are not of primary importance in governing its distribution. On his first visit to Jamaica the author noted that the species is most abundant in the red-soil

districts of Manchester Parish (as pointed out by T. H. Farr), and on his second visit he paid particular attention to edaphic factors in all *Phanaeus* localities, emerging with the impression that the species is practically limited in its distribution to the soils which result from the weathering of the White Limestone Formation (fig. 31). These soils range from dark brown through red to yellow-brown (Hose, 1951) and are uniformly porous and silty, often occurring in deep deposits. It is, undoubtedly, the physical properties of this soil which render it highly suitable for digging the deep burrows of the *Phanaeus*. There are still too few records for us to be sure about this edaphic factor. Some of the points on the distribution map (fig. 31) are based on "sightings" of burrows by the author and not directly on the capture of specimens. However, it is impossible to be mistaken about the highly characteristic earth mounds alongside cow dung, as there is no other large burrowing dung beetle in Jamaica.



Fig. 31, Distribution of *Phanaeus carnifex* (Linnaeus) in Jamaica in relation to the extent of the White Limestone Formation (white areas). Limits of the latter are taken from Hose (1951).

In the Agriculture Ministry farm at Grove Place, Manchester Parish, the degree of exploitation of the cow dung by this species is phenomenal. The beetles are so abundant that they enter into the barnyards and excavate in the entrances of barns, thus sometimes being crushed underfoot by the cows. Every pile of cow dung is completely exploited and quickly reduced to a red earth mound with only a few scraps of dried dung remaining at the surface. The feeding burrows of this species are unbranched and descend to a depth of 25-30 cm, where a food sausage is stored in the end. Nests were not

seen, but a brood ball in the Science Museum in Kingston, coated with a thick layer of red earth, measures 35 mm in diameter and 40 mm in height, and is of the pear shape normally seen in this genus (it was not opened).

Beetles are seen flying abundantly in the daytime, both in sunshine and rain. The female may frequently be seen transporting excrement over the surface of the ground by pushing it with the head and forelegs. Gosse (1848) says of this species (cited as *Phanaeus* sp. nov.): "Common on the roads, rolling pellets of horse dung; it chiefly occurs in the lowlands." The habit of pushing and rolling dung has earned this species the common name of "tumble bug," by which it is widely known.

Distribution. — Jamaica. Literature records citing this species from Cuba (Olsoufieff, 1924; Paulian, 1933) are based on a total of three rather old specimens, and it is curious that the latter author should consider this sufficient to establish the presence of this species "de façon certaine" in Cuba, in the face of negative results by a host of old and recent collectors on that island. Evidently, the three specimens were mislabelled and this species does not occur in Cuba. It has not been seen there by F. de Zayas (in litt.) in many years of active collecting.

The U. S. National Museum has two specimens bearing the label "Estero, Fla., 6-12 May 1908, Van Duzee." Further specimens will have to be collected before this species can be considered to be established in Florida.

Material examined. — 107 specimens. The author's material is deposited in ANSP, BMNH, MNHN, GH.

JAMAICA. St. Thomas Parish: Bath, C. R. Orcutt (2), [USNM]; St. Andrew Parish: Stony Hill, 1,300 ft, 16 October 1946, G. B. Thompson (1), [SMIJ]; St. Mary Parish: Carron Hall, 1,500 ft, 30 September 1952, W. St. John (1), [SMIJ]; St. Ann Parish: Moneague, 1,300 ft, 14 September 1917, H. Morrison (5), [BMNH], [USNM]; 4 mi SE of Moneague, 2 February 1937, Chapin and Blackwelder (4), [SMIJ]; St. Ann's Bay, sea level, 4 March 1952, J. R. McDermott (2), [SMIJ]; Manchester Parish: Newport, 1,500 ft, 21 February 1937 (1), [SMIJ]; Mandeville, 2,000 ft, 6 June 1949, J. M. Davis (4), [SMIJ]; 11 October 1964, E. G. Matthews and T. H. Farr (2); Shooters Hill, 1,500 ft, 25 May 1949, C. B. Lewis (1),

[SMIJ]; Grove Place, 1,500 ft, 11 October 1964, E. G. Matthews and T. H. Farr (11); St. Elizabeth Parish: Quickstep, 1,250 ft, 12-13 April 1949, R. P. Benoig (16), [SMIJ]; Bogue-Lilliput, 500 ft, 31 July 1965, E. G. Matthews (5); Mile 16, Black River-Malvern Rd, 2,200 ft, 1 August 1965, E. G. Matthews (4); Balaclava, C. R. Orcutt (10), [USNM]; Trelawny Parish: 10 mi S of Falmouth, Good Hope Estate, 250 ft, 12 May 1956, T. H. Farr (1), [SMIJ]; 12 mi S of Falmouth, Windsor Estate, 500 ft, 11 August 1956, B. and B. Valentine (1); St. James Parish: Snug Harbour, Montego Bay, 1910, E. A. Andrews (1), [USNM]; Rosehall, sea level, 18 January 1950, G. Scott (1); [SMIJ]; Niagara, 1,800 ft, 31 July 1965, E. G. Matthews (3); location not determined: Fearon's, 3 September 1920, C. C. Gowdey (2), [BMNH]; no further data: (11), [BMNH]; July 1905 (6), [USNM]; A. H. Ritchie (1), [USNM]; (9), [USNM].

Genus ATEUCHUS Weber

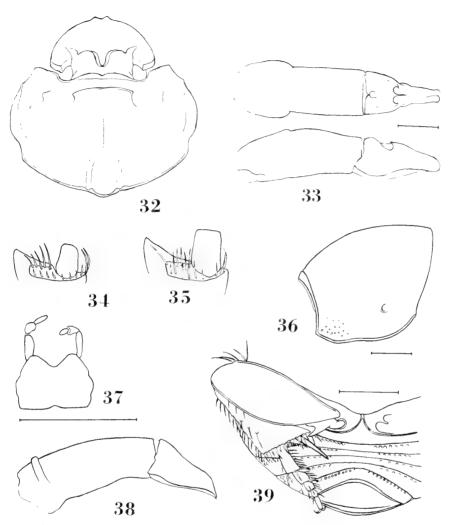
Ateuchus Weber, 1801, Observationes entomologiae, vol. 1, pp. 10, 37.

Type of genus. — Ateuchus histeroides Weber, 1801.

Description. — Small to medium sized beetles, oval, convex, nearly always uniformly black or bronze, unarmed. Clypeus obtusely bidentate, the teeth separated by a broad V-shaped emargination, genal margins obtusely angular, frons nearly always devoid of carinae, eyes above small, narrow. Mentum narrowed anteriorly, the apex not deeply emarginate. Labial palpi narrow, the basal segment the longest. Antennae nine-segmented, normal. Lateral fossae of pronotum round. Pronotum unarmed. Underside of prothorax anteriorly excavated to receive fore coxae. Hind edge of pronotum not margined, without large punctures. Scutellum absent. Eight elytral striae, epipleurae narrow. Mesosternum relatively long, about five times as wide as long. Meso-metasternal suture straight or feebly arcuate. Underside devoid of setae, the punctures tending to be cicatricose. Fore tibiae transversely truncated apically in both sexes, with three or four outer teeth, outer margin not serrate. Fore spur broadened in male. Hind tibia devoid of transverse carina on outer face. All tarsi present, five-segmented, claws present, small. Hind tarsal segments broad, triangular, first segment not elongated. Abdominal sternites not fused along midline, variable in relative lengths. entirely margined, basally with a strong, straight transverse carina.

Distribution. — Neotropical Region (\pm 70 species), Nearctic (5). In the Antilles (2 species): Grenada, Grenadines, St. Vincent, St. Lucia, Martinique, Guadeloupe, Montserrat, St. Christopher. Here recorded for the first time from St. Lucia and St. Christopher.

Remarks. — The origin and distribution of this genus are the



Figures 32-39. Fig. 32, Phanaeus carnifex (Linnaeus), \$\partial\$, fore body. Fig. 33, Phanaeus carnifex (Linnaeus), aedeagus in dorsal and lateral views. Fig. 34, Ateuchus illaesum (Harold), \$\delta\$, left fore spur and distal edge of fore tibia. Fig. 35, Ateuchus luciae n. sp., \$\delta\$, left fore spur and distal edge of fore tibia. Fig. 36, Ateuchus illaesum (Harold), lateral view of pronotum. Fig. 37, Ateuchus illaesum (Harold), labium. Fig. 38, Ateuchus illaesum (Harold), aedeagus. Fig. 39, Ateuchus illaesum (Harold), \$\delta\$, ventral view of right hind leg and part of abdomen.

same as those mentioned for *Phanaeus*, with an equal degree of penetration into the Nearctic. However, it has invaded the Lesser Antilles and not Jamaica. The extent of speciation in North America is probably far greater than the present number of described species indicates, as the Mexican and Central American forms have scarcely been studied. The species of *Ateuchus* are often very similar in general appearance and difficult to identify on the basis of existing literature.

Key to the Species of Ateuchus of the Antilles

Ateuchus illaesum (Harold)

- Choeridium illaesum Harold, 1868, Col. Hefte, vol. 4, p. 53; Arrow, 1903, Trans. Ent. Soc. London, 1903, pt. 4, p. 509; Leng and Mutchler, 1914, Bull. American Mus. Nat. Hist., vol. 33, p. 438; Blackwelder, 1944, United States Nat. Mus. Bull. 185, p. 204.
- Choeridium insulare Fleutiaux and Sallé, 1889, Ann. Soc. Ent. France, ser. 6, vol. 9, p. 395; Leng and Mutchler, 1914, Bull. American Mus. Nat. Hist., vol. 33, p. 438; Leng and Mutchler, 1917, Bull. American Mus. Nat. Hist., vol. 37, p. 207; Paulian, 1947, Coléoptères des Antilles, vol. 1, pp. 31-32. New synonymy.

Description. — Entirely black or rufo-piceous, sometimes with faint bronzing, shiny. Clypeo-genal suture marked by a fine impression for its entire length. Head surface finely and densely punctate in male, transversely rugose on clypeus in female. Edge of clypeus more broadly margined in female. Dorsal ocular areas small, separated by a distance equal to 14 times their width at base. Lateral edges of pronotum in dorsal view subparallel, slightly convex. In lateral view edge of pronotum is partially straight or even a little concave (fig. 36). Extreme lateral surfaces are vertical, not deflexed. Base of pronotum not margined. Pronotal surface smooth and very shiny, extremely finely punctate, the punctures well and evenly separated except on anterior angles, which are sometimes more densely and coarsely punctate. Median longitudinal sulcus clearly impressed on basal third only. Prosternum impunctate, without carinae. Mesosternum finely, densely but indistinctly punctate, tending to become rugose posteriorly, without median smooth area. Meso-metasternal suture feebly angulate. Mesepimera finely rugulose, with large, irregular, shallow punctures often C-shaped. Median lobe of metasternum smooth, extremely finely punctate; lateral lobes densely covered with large, shallow C-shaped cicatrices. Metepisterna finely rugulose and coarsely cicatricose. Elytra with striae distinct, impressed (more deeply so posteriorly), very finely and indistinctly crenato-punctate. Interstriae moderately convex, smooth and shiny, extremely finely punctate. Seventh stria as strongly impressed as remaining striae. Fore tibia outwardly with three large, broad teeth and an additional proximal toothlike expansion of margin. Fore spur rectangular in male (fig. 34), linear and distally truncated in female. and hind femora ventrally extremely finely punctate, completely margined on both anterior and posterior edges. Hind coxae with an incomplete row of setigerous punctures on hind border inwardly. Hind trochanters of male with a strong oblique spine issuing from posterior edge (fig. 39). First segment of middle and hind tarsi trapezoidal, equal in length to following two segments combined, all but first segment triangular. Abdominal sternites shortened but not fused medially, the sides basally with a row of large irregular punctures. Pygidial disc finely rugulose basally, otherwise smooth, very finely punctate, somewhat swollen in male, sometimes with a faint longitudinanl groove, not apparent in female. Aedeagus as in fig. 38. Total length 5.5-7.0 mm.

Type. — Mexico. Three specimens in MNHN; of *insulare:* Guadeloupe, MNHN.

Geographical variation. — Specimens from St. Vincent have a distinct cupreous tinge and are less shiny than the others. The elytral intervals are also slightly less convex and more coarsely punctate. A few males from Martinique have a faint longitudinal linear impression on the pygidial disc. Paulian (1947) noted that Martinican specimens have the elytral striae slightly less coarsely punctate than the ones from Guadeloupe, a difference barely perceptible to the present author and perhaps due to individual variation. No geographical size differences could be observed.

Remarks. — One of the three Harold types of illaesum in the Paris Museum was examined by the author and compared to a paratype of insulare Fleutiaux and Sallé. No differences could be seen. As a matter of fact, Harold (1868b) himself reported that he had seen a specimen of illaesum from Martinique. Arrow (1903) determined the Grenada and St. Vincent specimens as illaesum. Thus, with this species recorded from three different islands of the Lesser Antilles it is curious that Paulian (1947) should continue to refer to the specimens from Guadeloupe, Martinique, and Montserrat as in-

sulare Fleutiaux and Sallé, without making a comparison with illaesum.

Ecology. — This species is found in both open lowland pastures and lowland forests. Very low, flat pastures which tend to be flooded are avoided, as are those exposed to strong winds or salt spray. Otherwise both dry and moist pastures and woodlands up to about 700 ft elevation are exploited, sometimes intensively. At these low elevations A. illaesum is found together with Onthophagus antillarum Arrow (which has a much greater altitudinal range) on most of the islands, but the Ateuchus occurs in all types of soil, including sand, while the Onthophagus is restricted to loam or clay. Both fresh and old cow dung is exploited, as is horse dung and human excrement. Arrow (1903) reports that this species was collected in rotten fruit by H. H. Smith. It does not come to carrion-baited traps.

Distribution. — Mexico (Colima, Veracruz, and Chiapas according to Bates, 1887), Colombia (Harold, 1868b), Grenada, Grenadines, St. Vincent, Martinique, Guadeloupe, Montserrat, St. Christopher. Recorded for the first time from St. Christopher.

Material examined. — 308 specimens, including one of type series of *illaesum* and one paratype of *insulare*. The author's material is deposited in ANSP, BMNH, CNC, GH, MNHN, USNM.

GRENADA. St. George Parish: Mount Gay Estate, 500 ft, H. H. Smith (3), [BMNH]; Grande Anse, sea level, 8-9 July 1965, E. G. Matthews (67); Perseverance Estate, sea level, 8 July 1965, E. G. Matthews (2); Hog Island, 1 August 1935, S. T. Danforth (1), [USNM]; St. David Parish: Bacolet, sea level, 9 July 1965, E. G. Matthews (2); Westerhall Estate, sea level, 9 July 1965, E. G. Matthews (1); St. Andrew Parish: Balthasar, 500 ft, H. H. Smith (1), [BMNH]; no further data: (1), [BMNH].

GRENADINES. MUSTIQUE: H. H. Smith (3), [BMNH]; BEQUIA: 13 July 1965, E. G. Matthews (49); CARRIACOU: July 1935, S. T. Danforth (1), [USNM]; Sebastian Gates (1), [USNM].

ST. VINCENT. St. George Parish: South end, H. H. Smith (1), [BMNH]; Kingstown, H. H. Smith (1), [BMNH]; 2 mi N of Mesopotamia, 11 February 1936, R. E. Blackwelder (2), [USNM]; Greathead Bay, Sta. 167, 7 February 1936, R. E. Blackwelder (1), [USNM]; Yambu R., Sta. 170, 10 February 1936, R. E. Blackwelder (2), [USNM]; mi 85 Windward Rd., Sta. 181, 19 February 1936,

R. E. Blackwelder (8), [USNM]; St. Patrick Parish: Wallilabou, 300 ft, 10 July 1965, E. G. Matthews (27); 1.5 mi E of Wallilabou, 600 ft, 10 July 1965, E. G. Matthews (6); Chalmers Hill, 1 mi N of Layou, 600 ft, 11 July 1965, E. G. Matthews (4); St. Andrew Parish: Buccament R., 15 February 1936, R. E. Blackwelder (3), [USNM]; St. David Parish: Dark View Cemetery, 100 ft, 10 July 1965, E. G. Matthews (2); Troumaka, Sta. 175, 13 February 1936, R. E. Blackwelder (8), [USNM]; Charlotte Parish: .5 mi N of Colonarie, sea level, 11 July 1965, E. G. Matthews (3); 3 mi N of Orange Hill, Sta. 164, 4 February 1936, R. E. Blackwelder (14), [USNM]; no further data: H. H. Smith (39), [BMNH].

MARTINIQUE. 2 km N of St. Pierre, sea level, 30 May 1964, E. G. Matthews (17); Le Précheur, sea level, 20 December 1953, R. Pinchon (3), [RP]; Fort-de-France, sea level, July 1952, R. Pinchon (1), [RP].

GUADELOUPE. Basse Terre: 2 km S of Capesterre, Sta. 75, 30 October 1935, R. E. Blackwelder (1), [USNM]; no further data: Vitrac (1), [MNHN].

MONTSERRAT. 6 mi S of Plymouth, Sta. 262, 15 July 1936, R. E. Blackwelder (1), [USNM]; Woodlands, 250 ft, February 1959, G. R. Proctor (1), [SMIJ].

ST. CHRISTOPHER. Base Mt. Brimstone, sea level, 18 July 1965, E. G. Matthews (7); top Mt. Brimstone, 700 ft, 18 July 1965, E. G. Matthews (5); Belle Vue Estate, 100 ft, 18 July 1965, E. G. Matthews (3); Key Gut, 100 ft, 19 July 1965, E. G. Matthews (11); Sta. 306 (Key Gut), 13 February 1936, R. E. Blackwelder (1), [USNM]; no further data: July 1935, S. T. Danforth (1), [USNM].

Ateuchus luciae n. sp.

Description. — Entirely black, shiny. Clypeo-genal suture marked by a fine impression for its entire length. Head surface finely and densely punctate, faintly transversely rugose anteriorly in male, strongly rugose in female. Edge of clypeus more broadly margined in female. Dorsal ocular areas small, separated by a distance equal to about 17 times their width at base. Lateral edges of pronotum in dorsal view slightly converging anteriorly, slightly rounded, more strongly so anteriorly. In lateral view, edges of pronotum partially straight, very slightly less concave than in illaesum (fig. 36). Extreme lateral surfaces of pronotum vertical, not deflexed. Base of pronotum not margined. Pronotal surface smooth and very shiny, extremely finely

punctate, the punctures well and evenly separated, anterior angles slightly more coarsely punctate. Median longitudinal sulcus clearly impressed on basal third only. Prosternum impunctate, without carinae. Mesosternum densely punctate, the punctures tending to run into longitudinal rugae medially and posteriorly, without median smooth area. Meso-metasternal suture feebly arcuate or slightly angulate. Mesepimera very finely rugulose, with several rows of large C-shaped cicatrices. Median lobe of metasternum smooth, very finely punctate; lateral lobes densely covered with large shallow cicatrices. Metepisterna very finely rugulose and coarsely cicatrico-punctate. Elytral striae shallow, not at all impressed except at extreme posterior, very finely and indistinctly crenato-punctate. Interstriae completely flat, smooth and shiny, extremely finely punctate. Seventh stria as strongly impressed as remaining striae. Fore tibia outwardly with three large teeth and an additional proximal tooth-like projection of margin. Fore spur short and broad in male, quadrangular (fig. 35), in female elongated, linear, and distally truncated. Middle and hind femora ventrally extremely finely punctate, completely margined on both anterior and posterior edges. Hind coxae with incomplete row of irregular setigerous punctures on hind border inwardly. Hind trochanters of male with a strong oblique spine issuing from posterior edge, as in illaesum (fig. 39). Middle and hind tarsal segments triangular except for trapezoidal first segment, which in hind tarsus is equal in length to following two combined. Abdominal sternites shortened medially, sixth sternite shorter than previous two combined in male, equal to previous two combined in female. Sternites basally with a row of large irregular punctures, not setigerous. Pygidial disc very finely rugulose basally, otherwise smooth, very finely punctate, slightly swollen in male. Aedeagus as in illaesum (fig. 38). Total length 6.2-8.0 mm.

Type. — Gros Morne, St. Lucia. USNM.

Remarks. — This species is very close to illaesum Harold, found on adjacent islands, but may be told easily at a glance by its elytra, which appear to be almost unstriated to the naked eye, and usually also by its larger size. These two forms are considered to be separate species partly because of the ecological differences between them (see below). In appearance A. luciae resembles A. ampliatus (Bates) of Mexico, but the latter has no spine on the male trochanter and the basal pygidial groove is deeply impressed.

Ecology. — Unlike illaesum, this species is not found in typical open cow pastures or in sandy soil. It is more strictly a forest inhabiting species, occurring in both xerophytic and mesophytic forests of low altitudes (up to 1,000 ft, perhaps higher). It was trapped with human dung and was found naturally in cow dung in a shaded, cultivated hillside. It appears to be rare or highly localized.

Distribution. — St. Lucia.

Material Examined. — 32 specimens, deposited in ANSP. BMNH, CNC, MNHN, USNM.

ST. LUCIA. *Quarter of Castries:* Gros Morne, 2 mi SE of Castries, 1,000 ft, 15 July 1965, E. G. Matthews (15); 2 mi N of Castries, sea level, 16 July 1965, E. G. Matthews (3); *Quarter of Gros Ilet:* Gros Ilet, 30 July 1963 (14), [USNM].

Genus UROXYS Westwood

Uroxys Westwood, 1847, Trans. Ent. Soc. London, vol. 4, p. 229.

Type of genus. — Uroxys cuprescens Westwood, 1847.

Description. — Small or moderate-sized beetles (3-15 mm long), entirely dark, sometimes with cupreous reflections. Clypeus bi- or quadridentate. Dorsal ocular areas relatively large, the inner edges usually inwardly rounded. Prothorax below very deeply excavated anteriorly to receive fore femora, edge of pronotum here strongly folded upward, this producing a long longitudinal groove in pronotal surface near edge in most species. Base of pronotum not or finely margined, with a series of large shallow, usually longitudinal, punctures which are sometimes joined together to form a crenated border. Mesosternum long, about five times as wide as long at middle. Meso-metasternal suture feebly to very strongly angulate, sometimes strongly rounded. Margin accompanying meso-metasternal suture bent back laterally to form broad inner margins of mid-coxal cavities. Underside glabrous, cicatrico-punctate. Elytra with eight striae, surface between seventh and eighth stria often bent more or less sharply under, forming an edge which becomes more carinate posteriorly and is sometimes drawn out into posterior laminate projections in some species. Fore coxae transverse, fore femora elongated, much more so in male, with edges straight, fore tibiae scalpriform (terminally transversely truncated), with three feeble or moderate outer teeth, rest of outer margin not serrate. Middle and hind tibiae rather gradually expanding distally, sometimes with a transverse carina on outer face. Tarsi always present, five-segmented, the segments triangular, gradually diminishing distally, tarsal claws minute. Abdominal sternites not fused. Pygidium more or less deflexed, basally with a deep groove, the disc smooth, sometimes swollen.

Distribution. — Confined to the Neotropical Region, not extending northward beyond the tropical evergreen forest regions of Mexico. About 45 species, of which three are known from the Lesser Antilles, one of these also from Trinidad.

Remarks. — The genus *Uroxys* is remarkable for the nature of the sexual dimorphism, which involves the legs, pronotal edges, and elytra instead of the head and pronotal sculpturing, as in many Coprini.

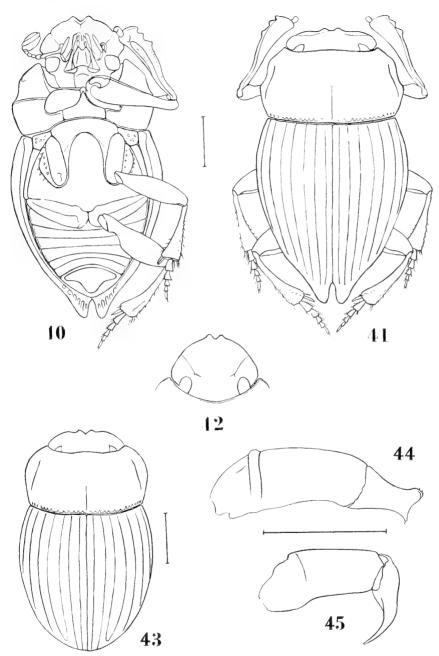
As presently constituted, the genus is somewhat heterogeneous, and includes, in addition to the small species such as those of the Antilles, some large ones with a cephalic carina and a strongly convex shape, with a consequent loss of the typical long, deep lateral pronotal groove and folded or carinate elytral edge between the seventh and eighth stria, and with a *Copris*-like transverse carina on the outer face of the hind tibia. The above description is compiled from various available works and attempts to encompass all the heterogeneous elements of the genus. The result is a nebulous generic concept which will have to be modified or made more precise by a revisional study.

The earliest generic revision is that of Harold (1868a), but it deals with only 10 of the 45 or so presently known species. The most recently available key is that of Arrow (1933), which does not include 10 species subsequently described by Balthasar (1940) and a few additional ones recently described. No recent work describes and compares all the known species together, hence it is difficult to identify new material. No worker has used the male genitalic characters, which promise to be useful at least in arriving at major subdivisions of the genus, judging by the difference in form between the genitalia of *U. productus* and *vincentiae* (figs. 44, 45).

Key to the Species of Uroxys of the Antilles

- 2'. Dorsal ocular areas large, broad, the distance between them equal to three times their width. Edge of clypeus with a small emargination flanking median teeth, giving impression of supplementary lateral teeth. Grenada, Trinidad trinitatis Arrow.

Figures 40-45. Fig. 40, *Uroxys productus* Arrow, &, ventral view. Fig. 41, *Uroxys productus* Arrow, &, dorsal view. Fig. 42, *Uroxys productus* Ar-



row, \hat{s} , head. Fig. 43, Uroxys productus Arrow, \hat{s} , body in dorsal view. Fig. 44, Uroxys productus Arrow, aedeagus. Fig. 45, Uroxys vincentiae Arrow, aedeagus.

Uroxys productus Arrow

Uroxys productus Arrow, 1933, Ann. Mag. Nat. His., ser. 10, vol. 11, p. 389; Paulian, 1939, Psyche, vol. 46, p. 141; Paulian, 1947, Coléoptères des Antilles, vol. 1, p. 32.

Description. — Elongate-oblong, sericeous. Clypeus bidentate, the teeth rounded and separated by a triangular emargination. Genal margins obtusely angulate (fig. 42). Head surface very finely shagreened, imparting a sericeous sheen, impunctate. Ocular areas with inner margins feebly rounded inwardly, distance between them 5-5½ times their width, canthus remote from inner edge. Hind edge of frons not margined. Underside of clypeus with a median process in form of a short transverse carina. Labium laterally rounded, narrowing apically, deeply emarginate. First and second palpal segments subglobose, the second a little smaller than first, third segment smallest, fusiform. Pronotum a little swollen, very finely shagreened, sericeous, impunctate, margined basally by a crenate line representing large shallow punctures merged with basal edge (fig. 41). Laterally punctures are separate. Lateral margins of pronotum strongly bent up anteriorly in lateral view, in dorsal view differing in the sexes. Median longitudinal sulcus of pronotum distinct, finely impressed basally. Lateral fossa in form of deep but short longitudinal sulcus. Mesosternum about five times as wide as long in middle, impunctate. Meso-metasternal suture strongly rounded (fig. 40). Middle coxal cavities somewhat oblique, margined inwardly on metasternum with very broad margins merging with meso-metasternal suture. Outwardly coxal margin is greatly expanded on lateral metasternal lobes (fig. 40). Median lobe of metasternum impunctate, lateral lobes with large shallow punctures on coxal margin and in a row along outer edge. Mesepimera with a few large punctures, metepisterna impunctate. Elytra with eight striae, seventh stria present for a little more than basal half of elytral length. Striae deeply and evenly impressed, very finely and remotely punctate, each stria terminating at outer edge of elytron, striae 3 and 4 distally joined, at least in female. Intervals convex, finely shagreened and alutaceous, impunctate. Edges of elytra just outside seventh stria bent inward, forming a lateral rounded ridge which becomes sharper posteriorly. Form of this ridge differing in the sexes. Fore tibiae with three outer distal teeth, rounded and not prominent, rest of outer margin not serrate. Distal end of fore tibiae transversely truncated. Fore spur straight, distally truncate. Fore tarsi small, linear. Form of fore legs differing in the sexes. Middle and hind femora impunctate, tibiae rather gradually expanded distally, flattened, devoid of strong carinae. Hind femora modified in male. Spurs short. Tarsal segments triangular, first segment larger than second, all segments gradually diminishing in size distally. Tarsal claws extremely small, slightly bent and basally angulate.

Abdominal sternites all about equal in length medially, impunctate. Basal margin of pygidium with two lateral rounded expansions separated from disc by a very deep trisinuate furrow (fig. 40). Disc of pygidium not strongly gibbous or swollen. Pygidium strongly inclined forward. Aedeagus with parameres distally bearing a dorsal prominence with small outwardly directed teeth and a ventral point with an apical tuft of setae (fig. 44). Total length 4.2-6.0 mm.

Sexual dimorphism. — Male (figs. 40 and 41): Lateral margins of pronotum angled out at juncture with pleural carina, strongly sinuate. Fore legs greatly elongated, fore tibiae basally sinuate. Fore spur three to four times as long as wide, sublinear, and truncated. Hind femora with posterior edge expanded and sinuate. Distal ends of elytra strongly drawn out into rounded lobes. Female (fig. 43): Lateral margins of pronotum rounded when seen from above. Fore legs only moderately elongated, the "elbows" only slightly surpassing pronotal edge. Fore tibiae not sinuate. Fore spur twice as wide as long, truncate. Hind femora normal. Distal ends of elytra rounded, but slightly carinate and prominent.

Type. — Tropical America. BMNH.

Remarks. — Arrow (1933) did not know the origin of the single male specimen on which he based the description of this species. Paulian (1939) first recorded the species from Guadeloupe on the basis of the two specimens described here, which he apparently compared with the type. In 1947 Paulian noted that these two specimens are distinctly smaller than the type, which measures 7 mm, but that otherwise they seem identical with it. The species is still known only from these three specimens; the author could not find it in Guadeloupe.

Ecology. — The male bears a label saying: "Rare, isolément sous les pierres en forêt." There are no longer any natural forests in the region of Trois Rivières, which is given over to the intensive cultivation of banana.

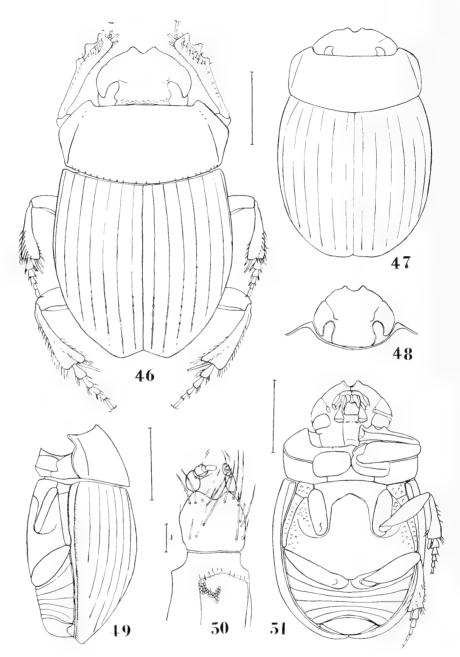
Distribution. — Guadeloupe.

Material examined. — Two specimens.

GUADELOUPE. Basse Terre: Trois Rivières, Dufau (1), [MNHN]; no further data: (1), [MNHN].

Uroxys vincentiae Arrow

Uroxys vincentiae Arrow, 1903, Trans. Ent. Soc. London, 1903, pt. 4, p. 510; Leng and Mutch'er, 1914, Bull. American Mus. Nat. His., vol. 33, p. 438; Blackwelder, 1944, United States Nat. Mus., Bull. 185, p. 204.



Figures 46-51. Fig. 46, *Uroxys vincentiae* Arrow, major &. Fig. 47, *Uroxys vincentiae* Arrow, minor & (paratype), body in dorsal view. Fig. 48, *Uroxys vincentiae* Arrow, minor & (paratype), head. Fig. 49, *Uroxys vin-*

Description. — Oval or oblong, very shiny, black, legs rufous. Clypeus bidentate, the teeth rounded, not prominent, emargination between them shallow, rounded (fig. 46). Head surface very finely punctate in male, clypeus transversely wrinkled in female. Ocular areas with inner margin sinuate, the distance between them equal to five times their width (fig. 48). Canthus remote from inner edge. Hind edge of head with transverse rows of coarse punctures. Underside of clypeus with a median process which is a Y-shaped carina. Labium narrowing apically, moderately emarginate, first palpal segment oval, larger than second, which is somewhat globose, third segment cylindrical, truncate (fig. 50). Pronotum very finely punctate, completely smooth and shiny between punctures, extremely finely margined basally and with a row of large shallow punctures. Form of lateral margins differing in the sexes. No trace of a median longitudinal sulcus. Mesosternum about five times as wide as long at middle, impunctate. Meso-metasternal suture strongly angulate (fig. 51). Middle coxal cavities somewhat oblique, margined inwardly on metasternum with very broad margins merging with meso-metasternal suture. Outwardly coxal margin extends as a curved groove on lateral metasternal lobes (fig. 51). Median lobe of metasternum impunctate, lateral lobes with large shallow cicatrices. Mesepimeron with a few large cicatrices. Metepisterna with a row of cicatrices. Elytral striae distinct but shallow, finely and remotely punctate, each stria terminating well before distal edge of elytron and not joining any other stria. Intervals flat, very finely punctate, completely smooth and shiny between punctures. Edges of elytra between seventh and eighth striae drawn out into a lateral rounded ridge which becomes sharper and more prominent posteriorly, especially in major males. Fore tibiae with three outer distal teeth rounded and not prominent, rest of outer margin not serrate. Distal end of fore tibia transversely truncate, hollowed out below, inner edge nearly straight. Form of fore spur differing in the sexes. Fore femora with edges nearly straight. Middle and hind femora impunctate, tibiae rather gradually expanding distally, flattened, devoid of strong carinae. Tarsal segments triangular, all segments gradually diminishing in size distally. Tarsal claws extremely small, moderately bent and basally angulate. Abdominal sternites impunctate. Basal margin of pygidium with two lateral rounded expansions separated from disc by a very deep trisinuate furrow (fig. 49). Disc of pygidium very strongly swollen, smooth and impunctate. Aedeagus with parameres strongly bent and drawn out into long processes (fig. 45). Total length 3.3-4.5 mm.

Sexual dimorphism. — Male: Surface of clypeus smooth, finely punctate. Lateral edges of pronotum drawn out into prominent angles (fig. 46), or only moderately so in minor males (fig. 47), strongly sinuate in lateral view. Fore-

centiae Arrow, minor & (paratype), lateral view of body. Fig. 50, Uroxys vincentiae Arrow, labium. Fig. 51, Uroxys vincentiae Arrow, minor & (paratype), ventral view.

legs moderately elongated, "elbows" barely surpassing pronotal edge. Fore spur five times as long as wide, linear, distally truncate. Distal edges of elytra moderately drawn out into rounded lobes (figs. 46, 47). Hind edge of hind femur slightly angled out. Abdominal sternites 2-6 equal in length. Female: Surface of clypeus strongly transversely wrinkled, lateral edges of pronotum not drawn out, less sinuate in lateral view. "Elbows" just reaching pronotal edge. Fore spur three times as long as wide, tapering, distally rounded. Hind femur normal. Distal edges of elytra not or barely drawn out. Abdominal sternites 5 and 6 longer than 2-4.

Type. — Cumberland, St. Vincent. BMNH.

Remarks. — Arrow (1903), in describing this species, notes that the disc of the clypeus is "without any trace of transverse wrinkles." This holds true for the males only, and presumably both the specimens seen by Arrow were males (the paratype examined by the present author is a minor male). After the above modification is made, the only features which continue to separate this species from *Uroxys trinitatis* Arrow are an absence of a distinct emargination outside the clypeal teeth and the narrower ocular areas.

Ecology. — All localities in which the author collected this species were lowland forests near the sea, both xerophytic and moist. It comes to human and cow excrement, but not to carrion. It appears to be very rare in both Grenada and St. Vincent, where only one and two specimens were collected respectively in eight days' trapping, while in Bequia a single night's trapping yielded 45 specimens of this species. The author's St. Vincent locality (Wallilabou) is only about a mile distant from Smith's locality (Cumberland).

Distribution. — Grenada, Grenadines, St. Vincent. Recorded here for the first time from Grenada and the Grenadines.

Material examined. — 50 specimens including one paratype. The author's material is deposited in ANSP, BMNH, CNC, GH, MNHN, USNM.

GRENADA. St. George Parish: Grande Anse, sea level, 9 July 1965, E. G. Matthews (1).

GRENADINES. CARRIACOU: sta. 144, 17 January 1936, R. E. Blackwelder (1), [USNM]; BEQUIA, 12 July 1965, E. G. Matthews (45).

ST. VINCENT. *St. Patrick Parish:* Cumberland, hillside near sea, 30 September, H. H. Smith (1), [BMNH]; Wallilabou, 200 ft, 11 July 1965, E. G. Matthews (2).

Uroxys trinitatis Arrow

Uroxys trinitatis Arrow, 1933, Ann. Mag. Nat. His., ser. 10, vol. 11, p. 391; Blackwelder, 1944, United States Nat. Mus. Bull. 185, p. 204.

A female apparently belonging to this species and collected near the Grand Etang in Grenada was sent to the author by Dr. P. W. Hummelinck. The specimen agrees with the description of *U. trinitatis* Arrow and keys to it in Arrow (1933) on the basis of the size of the eyes (dorsal ocular areas), which are larger than those of *vincentiae* Arrow but smaller than those of *pygmaeus* Harold. The latter species, in any case, has convex elytral intervals, according to Balthasar (1940). Unequivocal determination of this specimen is not possible because it is a female and because the edge of the clypeus is damaged. Nevertheless it appears identical to another female *trinitatis* sent by Dr. Hummelinck from Trinidad.

The specimen is readily separable from *vincentiae* by the size of the ocular areas, as noted in the key. The feature of the clypeal edge is less obvious and can be seen only in direct comparison. In other respects the two species seem identical in the female sex.

The author set traps extensively in the area of the Grand Etang without collecting this species. Its habitat is quite distinct from that of *vincentiae*, consisting of dense montane forest, partly windswept and evidently subject to moderate, but not heavy, rainfall.

Distribution. — Trinidad, Grenada. Here recorded for the first time from Grenada.

Material examined. — One specimen.

GRENADA. *St. Andrew Parish:* near Grand Etang, 500 m, 24 January 1955 (1), [ZLRU] (now deposited in Rijksmuseum van Natuurlijke Historie in Leiden).

Genus CANTHOCHILUM Chapin

Canthochilum Chapin, 1934, Proc. Biol. Soc. Washington, vol. 47, p. 99;
Chapin, 1935, J. Agr. Univ. Puerto Rico, vol. 19, p. 67; Paulian, 1939, Psyche, vol. 46, p. 145; Blackwelder, 1944, United States Nat. Mus. Bull. 185, p. 202; Wolcott, 1948, J. Agr. Univ. Puerto Rico, vol. 32, p. 247; Pereira and Martínez, 1956, Rev. Brasileira Ent., vol. 6, p. 134; Matthews, 1963, Coleopt. Bull., vol. 17, p. 110; Matthews, 1965, Trans. American Ent. Soc., vol. 91, p. 431; Zayas and Matthews, 1966, Poeyana, Ser. A, No. 14, pp. 1-24.

Type of genus. — Canthochilum oakleyi Chapin, 1934.

Description. — Broadly oblong or oval. Clypeus with four or six teeth, an additional small tooth on gena at clypeo-genal suture. Dorsal ocular areas variable. Hind edge of head not margined. Antennae nine-segmented. Labium narrowing distally, the sides forming an obtuse rounded angle, the apical edge with a feeble rounded emargination (figs. 69-71). Labial palpi with basal segment trapezoid, small, second segment oval, much larger, third segment cylindrical, smallest (fig. 71). Pronotum with lateral edges basally subparallel or converging anteriorly, straight, abruptly bending in at anterior third. Base of pronotum not margined. Propleura anteriorly very deeply excavated to receive fore femora. Mesosternum about three to four times as wide as long. Meso-metasternal suture moderately angulate or evenly arcuate. Margins of mid-coxae on median lobe of metasternum often broad, merging with mesometasternal sutural margin to form a single angular line which continues around mid-coxal cavities and forms a more or less broad outer coxal margin on lateral lobes of metasternum (figs. 59-65). Elytra long, not leaving pygidium visible in direct dorsal view, the striae basally more or less equidistant, surface of elytron just outside seventh stria abruptly deflexed, forming a more or less distinct lateral elytral carina (except in C. cemi Zayas and Matthews). Elytra with eight striae, sometimes obsolete. Fore tibia with three outer teeth, the rest of edge finely serrate. Distal end of tibia variable, transversely or obliquely truncated. Middle and hind tibiae gradually broadening distally. Middle and hind tarsal segments trapezoidal or subtriangular, first segment of hind tarsus a little longer than second. Tarsal claws strongly bent, basally not dentate but with a distinct angulation of edge. Pygidium with strong basal margin. Aedeagus with greatly reduced parameres, distal end of basal piece often ornamented (figs. 72-81).

Distribution. — Cuba and Puerto Rico.

Remarks. — The affinities of this genus are difficult to ascertain at present. It appears to have little in common with other more typical canthonine genera, since it possesses such special features as the enlarged second palpal segment of the labium, the distally widened middle and hind tibiae, long mesosternum, broad mid-coxal margins on median lobe of metasternum (in some species), inflexed elytral edges, forming a carina in all but one species, and the unusual form of the male genitalia. In the author's opinion, the affinities of this genus are not to be sought with typical canthonine genera so much as with Ipselissus and small dichotomines such as Bdelyrus, Trichillum, Pedaridium, Uroxys, Zonocopris, etc., with which it shares most of the features mentioned above. One need only compare Canthochilum with a small Uroxys such as U. vincentiae Arrow to note strik-

ing similarities, not only in general facies but also in such details as the form of the prothorax, meso- and metasternum (compare figs. 51 and 59), the elytra, both possessing a carina or ridge between the seventh and eighth stria, and the fact that sexual dimorphism may be seen in the legs. Even the tibiae, on the form of which the tribal separation is based, are not very different. The similarity between Bdelyrus and Canthochilum was noted in passing by Paulian (1939) in his description of B. bowditchi Paulian (now placed in Bdelyropsis Pereira, Vulcano, and Martínez).

The South American canthonine genus Ipselissus Olsoufieff seems to be the most closely related genus to Canthochilum in the New World. The author does not know this genus in natura, but the detailed description of *I. silphoides* (Harold) given by Martínez (1954) leaves no doubt of the closeness of the relationship. In fact, there seem to be no important differences between the two genera other than the absence of a lateral elytral carina in *Ipselissus* and its dentate tarsal claws. But one species of Canthochilum (cemi Zayas and Matthews) does not have this carina, and this genus has angulate tarsal claws not very different from those of Ipselissus. Martínez noted the similarity between Ipselissus and such dichotomine genera as Zonocopris, Pedaridium, Trichillum, and Uroxys, and suggested that Ipselissus occupies a transitional position between the sub-tribes Canthonina and Dichotomina. Canthochilum similarly occupies such an intermediate position, together with a number of Old World tropical genera such as Panelus, Pycnopanelus, and some species of Cassolus. The male genitalia would give us important clues, but unfortunately these have not been examined for any of these genera other than Canthochilum.

In any case, no final decisions can be arrived at regarding these small genera until their behavior is known, particularly until we know whether they make and roll balls or not. The proposal that *Canthochilum* stands in an intermediate position between the Scarabaeini and Coprini received strong support from the author's observations (Matthews, 1965) that Puerto Rican species of this genus roll balls only a short distance and bury them deeply. One species (*oakleyi* Chapin) apparently does not make balls at all. Further clues were obtained from the larval morphology of one species, which showed a remarkable mixture of features seen in several genera of three dif-

ferent tribes (Matthews, 1963). The author's personal opinion (not well substantiated at present) is that *Canthochilum* is a very primitive genus standing at the point of divergence of the subtribes Canthonina (Tribe Scarabaeini) and Dichotomina (Tribe Coprini).

The distribution of this genus, restricted to Cuba and Puerto Rico, is unique and is interpreted here as a relict pattern. The genus presumably once occurred at least on Hispaniola, where it is now either extinct or reduced to as-yet-undiscovered relict pockets. If it were as abundant on Hispaniola as it is in both Cuba and Puerto Rico, at least a few specimens would have shown up in the author's traps. The presence on Hispaniola of the genus *Canthon* (absent from Cuba and Puerto Rico) may have been instrumental in the presumed extinction there of *Canthochilum*.

Two recent papers (Zayas and Matthews, 1966 and Matthews, 1965) have dealt with the species of *Canthochilum* of Cuba and Puerto Rico respectively, hence the treatment accorded this genus here is greatly restricted. However, the opportunity is taken to present an overall view of the adaptations of the species of the genus, which is by far the most interesting of all Antillean Scarabaeinae because of the extensive adaptive radiation it has undergone.

The first fact that strikes the observer is the high degree of taxonomic isolation of most of the species. Two is the maximum number of species which can be grouped closely together. Such closely
related species pairs are histeroides Harold and cemi Zayas and Matthews from Cuba, and andyi Chapin and taino n. sp. from Puerto
Rico. Aside from these four, all other species are taxonomically
quite isolated. It is not even possible to group all the species from
one island together in any way except for the fact that all the Puerto
Rican species show sexual dimorphism in the form of the legs, while
none of the Cuban species do. This condition may show a common
origin for the Puerto Rican species, but it could also have been acquired through common selective pressures.

The adaptive radiation which the genus has undergone on both islands is largely eco-geographic, that is, the species have become adapted to live in different ecological zones by having (presumably) evolved different physiological tolerances for the temperature-humidity factors of the environment. There is no evidence for any food specialization and only one clear instance each of behavioral spe-

cialization (oakleyi) and a shift to daytime activity (guayca). However, it should be emphasized that much remains to be learned in these respects.

In general we have, first, species adapted to live in lowland for-These live under relatively fluctuating temperature est and scrub. and humidity conditions and some of them are both ecologically and geographically widespread on their respective island (i.e., they are The Cuban lowland or eurytopic species are eurytopic species). histeroides (Harold), gundlachi (Harold), and pijirigua Zavas and Matthews, and the Puerto Rican ones are boringuensis Matthews and taino n. sp. Secondly we have species adapted to live at moderate altitudes under more humid and less variable montane conditions (all stenotopic species, which do not occur in the lowlands). In Cuba these are tureyra Zayas and Matthews, baracutey Zayas and Matthews, cemi Zayas and Matthews, and anacaona Zayas and Matthews, and in Puerto Rico oakleyi Chapin and andyi Chapin. The geographical distribution of the stenotopic species follows two very different patterns in Cuba and Puerto Rico because of the different topography In Cuba the stenotopic species tend to be isolated of the islands. each in one or two (different) mountain ranges (as far as we know) (fig. 52), while in Puerto Rico they are more or less island-wide, but restricted to clearly defined altitude belts (see Matthews, 1965, for maps).

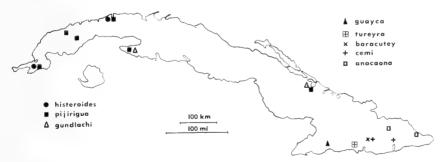


Fig. 52, Distribution of the species of Canthochilum in Cuba.

In the third ecological category we have species restricted to the highest altitudes on their respective islands. These are presumably adapted to withstand continuous low temperatures and high humid-

ity. Only one species is known in this category on each island: guayca Zayas and Matthews in Cuba and hispidum Chapin in Puerto Rico. The former species appears to be restricted to a single mountain, as far as we know: Pico Cuba in the Turquino massif, the highest mountain massif in Cuba. It was collected at an altitude of about 6,000 ft, which is the altitude record for any Antillean scarabaeine. C. hispidum, on the other hand, is found throughout the mountain ranges of Puerto Rico at elevations which start at only 1,500 ft in the east but climb to nearly 4,000 ft in the west-center at Cerro de Punta, the highest point on the island. It forms three geographical subspecies: if guayca is found on other mountains it will probably also be seen to form geographical subspecies. It is significant that both guayca and hispidum are flightless, unlike any other species of the genus. C. guayca has the wings almost totally atrophied, while hispidum is merely brachypterous but clearly flightless. However, the resemblance between the two species ends at this point. C. guayca is glabrous, intensely black with red humeri, and the dorsal ocular areas are greatly reduced. All these features leave no doubt that the species is active during the daylight hours. C. hispidum, on the other hand, is densely covered with capitate setae, brown, and the ocular areas are large. It is active at night, like most or all Canthochilum except guayca.

The color pattern of *guayca* gives it a superficial resemblance to the species of *Canthonella*, which are probably all diurnal. There is evidently a selective advantage to developing a red- or white-on-black color pattern in these diurnal canthonines (see also under *Onthophagus a. albicornis* above), although we cannot guess what this advantage might be at present.

Figures 53-71. Fig. 53, Canthochilum histeroides (Harold), head of holotype. Fig. 54, Canthochilum anacaona Zayas and Matthews, head. Fig. 55, Canthochilum guayca Zayas and Matthews, head. Fig. 56, Canthochilum pijirigua Zayas and Matthews, head. Fig. 57, C. pijirigua, octodentate form of head. Fig. 58, Canthochilum gundlachi (Harold), head of holotype. Fig. 59, Canthochilum histeroides (Harold), ventral view of holotype; mcx — inner midcoxal margin of metasternum. Fig. 60, Canthochilum anacaona Zayas and Matthews, \$\parpli \$, meso- and metasterna and abdominal sternites. Fig. 61, Canthochilum guayca Zayas and Matthews, meso- and metasterna. Fig. 62, Canthochilum pijirigua Zayas and Matthews, form 1, meso- and metasterna. Fig. 63, Canthochilum pijirigua Zayas and Matthews, form 2, meso- and metasterna. Fig. 64, Canthochilum gundlachi (Harold), holotype, meso- and metasterna.

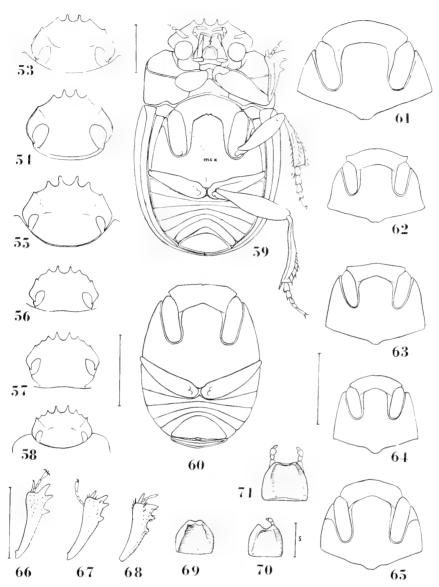


Fig. 65, Canthochilum oakleyi Chapin, meso- and metasterna. Fig. 66, Canthochilum guayca Zayas and Matthews, right front tibia and tarsus. Fig. 67, Canthochilum anacaona Zayas and Matthews, right front tibia and tarsus. Fig. 68, Canthochilum pijirigua Zayas and Matthews, right front tibia and tarsus. Fig. 69, Canthochilum histeroides (Harold), labium of holotype (palpi missing). Fig. 70, Canthochilum gundlachi (Harold), labium of holotype (right palpus not shown). Fig. 71, Canthochilum cakleyi Chapin, labium.

All of the species of *Canthochilum*, without exception, are leaf-litter inhabitants (patobionts) and occur only in forests or dense scrub. All the Cuban species were collected by Ing. F. de Zayas by processing litter in Berlese funnels, while all the Puerto Rican species were collected by the present author with dung-baited traps set in the leaf litter of forests.

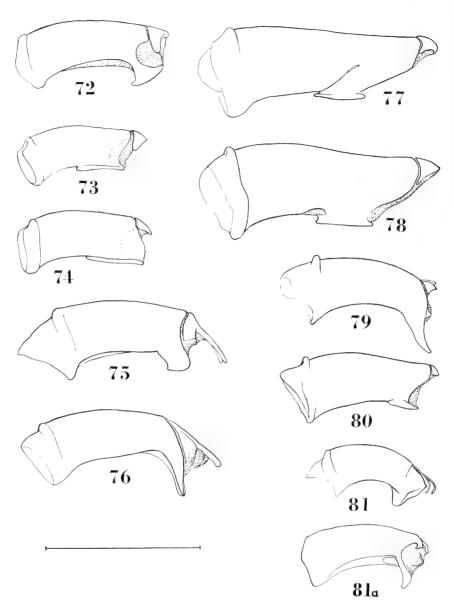
The following key to species is combined from Matthews (1965) and Zayas and Matthews (1966) and is modified to include characters of the male genitalia of ten species. The genitalia of the remaining three species could not be examined for lack of sufficient material at hand. The above-mentioned papers should be consulted for full descriptions and ecological data regarding these forms. Only the single new Puerto Rican species (taino n. sp.) is described here.

Key to the Species of Canthochilum

Cuban species

1.	Cuban species
1'.	Puerto Rican species
2(1).	Head with only six distinct teeth, margin between second and third pair of teeth evenly concave (figs. 53-55)
2'.	Head with eight teeth, the third pair sometimes very small or represented by an outward bend of margin (figs. 56-58)
3(2).	Fore tibia with distal edge straight, perpendicular to inner edge (fig. 68)
3'.	Fore tibia with distal edge angulate, bending obliquely forward (figs. 66, 67)
4(3).	Elytral striae impressed, interstriae convex; pronotum with anterior margin interrupted and bent backward to form a broad, shallow median depression; two short, sharp striae on head between eyes
4'.	Elytral striae feeble, interstriae flat; without pronotal depression or cephalic striae
5(4').	Elytra laterally completely devoid of a marginal carina alongside seventh stria; elytral striae nearly obsolete; clypeo-genal suture not marked by a carina; fore spur of male terminating in two small teeth; aedeagus of male in lateral view with basal piece terminating
	in two long, acute processes (fig. 76)
5'.	Elytra laterally normal for genus, with marginal carina; elytral striae feeble but distinct; clypeo-genal suture marked by a fine carina; fore spur of male apically rounded; aedeagus of male in lateral view with basal piece terminating in a shorter, broad process (fig. 75)

6(3').	Ocular areas small, separated by a distance equal to six times their width (fig. 55); meso-metasternal suture evenly arcuate (fig. 61); elytra convex; apterous; body intensely black with humeral angles and inflexed surfaces of elytra reddish; aedeagus with basal piece terminating in a broad pelecyform process (fig. 72)
6'.	Ocular areas larger, separated by a distance equal to two to four times their width; meso-metasternal suture angulate (fig. 60); winged; body uniformly dark
7(6').	Ocular areas normal, separated by a distance equal to three to four times their width; last abdominal sternite not greatly elongated; elytra dorsally moderately convex, marginal carina not continued posteriorly as a sharp ridge; surfaces shiny; aedeagus as in fig. 81atureyra Zayas and Matthews.
7'.	Ocular areas very large, separated by a distance equal to two to three times their width (fig. 54); last abdominal sternite greatly elongated (fig. 60); elytra dorsally flattened, marginal carina continued posteriorly as a ridge which extends nearly to suture; surfaces opaque
8(2').	A distinct, sharp transverse ridge on fronto-clypeal demarcation just inside anterior edge of eye (fig. 58); head always distinctly octodentate (fig. 58); pronotum densely and coarsely punctate, the punctures separated by a distance equal to 1-2 times their diameter and tending to run together into longitudinal grooves basally: elytral interstriae distinctly convex, rugulose gundlachi (Harold).
8'.	Fronto-clypeal demarcation without any sharp transverse ridge near eye; head sometimes not distinctly octodentate (fig. 56): pronotum more finely punctate, the punctures more separated and not running together into grooves; elytral interstriae completely flat or very slightly convex pijirigua Zayas and Matthews.
9(1').	Dorsal surfaces covered with a dense vestiture of capitate hairs which usually hold a layer of soil; elytra posteriorly each with two or three tubercles; aedeagus with basal piece tapering distally, parameres normal for genus (fig. 77)
9'.	Dorsal surfaces not covered with hairs; elytra without distal tubercles
10(9').	Lateral lobe of metasternum traversed anteriorly by a curved ridge which is an outward bend of mid-coxal cavity margin (fig. 65); relatively large beetles (6-8 mm in length) with male showing dimorphic features in fore and middle legs; aedeagus distally tapering, parameres normal (fig. 78)
10′.	Lateral lobe of metasternum with margin closely paralleling outer edge of mid-coxal cavity; smaller beetles (2.3-6.2 mm in length); male showing dimorphic features on hind legs only; aedeagus not tapering



Figures 72-81. Fig. 72, Canthochilum guayca Zayas and Matthews, aedeagus; membranes indicated by stippling. Fig. 73, Canthochilum pijirigua Zayas and Matthews, aedeagus of form 1. Fig. 74, Canthochilum pijirigua Zayas and Matthews, aedeagus of form 2. Fig. 75, Canthochilum histeroides (Harold), aedeagus. Fig. 76, Canthochilum cemi Zayas and Matthews, aedeagus. Fig. 77, Canthochilum hispidum Chapin, aedeagus. Fig. 78, Canthochilum oakleyi

- 11(10'). Lateral elytral carina continuing around entire edge of elytron nearly to median suture; elytral striae obsolete; aedeagus with basal piece distally expanded and parameres reduced to a pair of slender filaments (fig. 81) boringuensis Matthews.
- 11'. Lateral elytral carina terminating about two thirds of the way down elytral length; elytral striae distinct; parameres normal12

Canthochilum baracutey Zayas and Matthews

Canthochilum baracutey Zayas and Matthews, 1966, Poeyana, Ser. A, No. 14, p. 11.

Type. — Florida Blanca, Songo Oriente, Cuba. FZ. Unique. Distribution. — The type locality only.

Canthochilum tureyra Zayas and Matthews

Canthochilum tureyra Zayas and Matthews, 1966, Poeyana, Ser. A, No. 14, p. 12.

Type. — Loma del Gato, El Cobre, Oriente, Cuba. FZ. Distribution. — The type locality only.

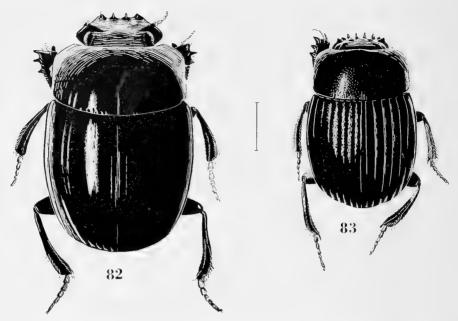
Canthochilum cemi Zavas and Matthews

Canthochilum cemi Zayas and Matthews, 1966, Poeyana, Ser. A, No. 14, p. 7.

Type. — Palma Mocha, Sierra Maestra, Cuba. FZ. Paratypes also in USNM and Universidad de Oriente, Santiago, Cuba.

Distribution. — Palma Mocha, Florida Blanca, Guantánamo, and Santa María de Loreto, all in Oriente.

Chapin, aedeagus. Fig. 79, Canthochilum andyi Chapin, aedeagus. Fig. 80, Canthochilum taino n. sp., aedeagus. Fig. 81, Canthochilum borinquensis Matthews, aedeagus. Fig. 81a, Canthochilum tureyra Zayas and Matthews, aedeagus.



Figures 82-83. Fig. 82, Canthochilum histeroides (Harold), holotype. Fig. 83, Canthochilum gundlachi (Harold), holotype.

Canthochilum histeroides (Harold)

Canthon histeroides Harold, 1868, Col. Hefte, vol. 4, p. 80; Leng and Mutchler, 1914, Bull. American Mus. Nat. His., vol. 33, p. 438; Balthasar, 1939, Fol. Zool. Hydrobiol., vol. 9, p. 224.

Canthochilum histeroides (Harold), Zayas and Matthews, 1966, Poeyana, Ser. A, No. 14, p. 4.

Type. — Cuba. MNHN.

Distribution. — Collected by Zayas on the north coast of Havana province (Río Santa Ana) and the peninsula of Guanahacabibes in Pinar del Río.

Canthochilum guayca Zayas and Matthews

Canthochilum guayca Zayas and Matthews, 1966, Poeyana, Ser. A, No. 14, p. 8.

Type. — Pico Cuba, Macizo Turquino, Oriente, Cuba. FZ. Paratypes also in USNM.

Distribution. — The type locality only.

Canthochilum anacaona Zayas and Matthews

Canthochilum anacaona Zayas and Matthews, 1966, Poeyana, Ser. A, No. 14, p. 8.

Type. — Yunque de Baracoa, Oriente, Cuba. FZ. Paratype also in USNM.

Distribution. — Sierra de Cristal and Yunque de Baracoa, Oriente.

Canthochilum gundlachi (Harold)

Canthon gundlachi Harold, 1868, Col. Hefte, vol. 4, p. 80; Leng and Mutchler, 1914, Bull. American Mus. Nat. His., vol. 33, p. 438.

Canthochilum gundlachi (Harold), Chapin, 1934, Proc. Biol. Soc. Washington, vol. 47, p. 101; Blackwelder, 1944, United States Nat. Mus. Bull. 185, p. 202; Zayas and Matthews, 1966, Poeyana, Ser. A, No. 14, p. 5.

Plesiocanthon gundlachi (Harold), Balthasar, 1939, Fol. Zool. Hydrobiol., vol. 9, p. 224.

Type. — Cuba. MNHN.

Distribution. — Collected by Zayas in the peninsula of Guana-hacabibes in Pinar del Río and near Santa Lucia on the north coast of Camagüey.

Canthochilum pijirigua Zayas and Matthews

Canthochilum pijirigua Zayas and Matthews, 1966, Poeyana, Ser. A, No. 14, p. 13.

Type. — El Pinar, Los Palacios, Pinar del Río, Cuba. FZ. Paratypes also in USNM.

Distribution. — In Pinar del Río: Monte El Pinar, Viñales, Guanahacabibes; in Santa Clara: Zapata peninsula; in Havana province: Río Santa Ana; in Camagüey: Playa El Inglés near Santa Lucía.

Remarks. — This widespread species can be divided into two poorly-defined groups which the authors at first considered separate species. However, the two forms are completely sympatric and until a more thorough study can be made of the variation of pijirigua it seems best to treat both forms as a single species. Most specimens may be separated as follows: form 1, inner margin of mid-coxal cavities straight, meeting meso-metasternal suture at a distinct angle (fig.

62), pronotal punctures rather large and separated by a distance equal to 2-3 times their diameter, clypeo-genal suture marked by a fine ridge, and aedeagus with distal edge of basal piece concave (fig. 73); form 2, inner margin of mid-coxal cavities curved, meeting meso-metasternal suture in an even curve (fig. 63), pronotal punctures finer, separated by a distance equal to 3-4 times their diameter, clypeo-genal suture not marked by a fine ridge, and aedeagus with distal edge of basal piece concave (fig. 74). The type belongs to form 1.

Canthochilum hispidum hispidum Chapin

Canthochilum hispidum Chapin, 1935, J. Agr. Univ. Puerto Rico, vol. 19, p. 67; Blackwelder, 1944, United States Nat. Mus. Bull. 185, p. 202; Wolcott, 1948, J. Agr. Univ. of Puerto Rico, vol. 32, p. 247; Matthews, 1963, Coleopt. Bull., vol. 17, p. 110; Matthews, 1965, Trans. American Ent. Soc., vol. 91, p. 436.

Type. — Villalba, Puerto Rico. USNM. Distribution. — The type locality only.

Canthochilum hispidum iunceanum Matthews

Canthochilum hispidum iunceanum Matthews, 1965, Trans. American Ent. Soc., vol. 91, p. 438.

Type. — Luquillo Forest, Puerto Rico. USNM. Paratypes also in AM, ANSP, BMNH, CNC, GH, USNM, Museum of Comparative Zoology, and Departamento de Zoologia (São Paulo).

Distribution. — Luquillo Range from 1,450 to 2,900 ft altitude.

Canthochilum hispidum serropunctae Matthews

Canthochilum hispidum serropunctae Matthews, 1965, Trans. American Ent. Soc., vol. 91, p. 436.

Type. — Cerro de Punta, Puerto Rico. USNM. Paratypes also in AM, ANSP, BMNH, CNC, GH, MNHN, USNM, Museum of Comparative Zoology, and Departamento de Zoologia (São Paulo).

Distribution. — Cerro de Punta and Monte Guilarte, 3,500 to 4,100 ft altitude.

Canthochilum oakleyi Chapin

Canthochilum oakleyi Chapin, 1934, Proc. Biol. Soc. Washington, vol. 47, p. 99; Blackwelder, 1944, United States Nat. Mus. Bull. 185, p. 202; Wolcott, 1948, J. Agr. Univ. Puerto Rico, vol. 32, p. 247; Pereira and Martínez, 1956, Rev. Brasileira Ent., vol. 6, p. 134; Matthews, 1965, Trans. American Ent. Soc., vol. 91, p. 439.

Type. — Adjuntas, Puerto Rico. USNM 50519. Distribution. — Cordillera Central at 2,100 to 3,500 ft altitude.

Canthochilum boringuensis Matthews

Canthochilum borinquensis Matthews, 1965, Trans. American Ent. Soc., vol. 91, p. 441.

Type. — 6 km west of Bayamón, Puerto Rico. USNM. Paratypes also in AM, ANSP, BMNH, CNC, GH, MNHN, USNM, Museum of Comparative Zoology, and Departamento de Zoologia (São Paulo).

Distribution. — Low altitude belt of Puerto Rico (Matthews, 1965).

Canthochilum andyi Chapin

Canthochilum andyi Chapin, 1935, J. Agr. Univ. Puerto Rico, vol. 19, p. 68; Blackwelder, 1944, United States Nat. Mus. Bull. 185, p. 202; Wolcott, 1948, J. Agr. Univ. Puerto Rico, vol. 32, p. 247; Matthews, 1965, Trans. American Ent. Soc., vol. 91, p. 442.

Type. — Matrullas Dam, near Orocovis, Puerto Rico. USNM 51080.

Distribution. — Intermediate altitude belt of Puerto Rico (Matthews, 1965).

Canthochilum taino n. sp.

Canthochilum histeroides auct. (nec Harold, 1868), Chapin, 1934, Proc. Biol. Soc. Washington, vol. 47, p. 101; Blackwelder, 1944, United States Nat. Mus. Bull. 185, p. 202; Wolcott, 1948, J. Agr. Univ. Puerto Rico, vol. 32, p. 247; Matthews, 1963, Col. Bull., vol. 17, p. 110; Matthews, 1965, Trans. American Ent. Soc., vol. 91, p. 444.

Description. — Broadly oblong, brown to black, legs paler. Dorsal surface of head uniformly extremely finely punctate. Clypeus quadridentate, the teeth acute, about equally spaced. Dorsal ocular areas large, separated by a

distance equal to four times their maximum width. Pronotal surface finely and evenly punctate, more or less finely shagreened, ranging from shiny to sericeous. Meso-metasternal suture broadly angulate, marked by a carina which continues posteriorly to delimit a fairly broad margin along mid-coxal cavities. Elytral striae distinct but not impressed, with very fine punctures regularly spaced along their length, sometimes impunctate on disc, the punctures becoming coarser posteriorly. Intervals flat, impunctate, shagreened, with a low callosity on second interval near base. Lateral elytral carina extending for less than three quarters of elytral length. Fore tibia with only a very small tooth at tarsal insertion. Distal end of fore tibia angulate, bending obliquely forward. All femora impunctate. Setae on middle and hind tibiae not forming continuous fringes. Sutures between abdominal sternites with a shallow pit near lateral ends. Pygidium impunctate. Aedeagus as in fig. 80. Total length 2.6-4.9 mm.

Sexual dimorphism. — Male: Pronotal edges subparallel, fore spur broadened slightly, fore tibia slightly bent in at middle, hind femora broadened, and hind tibiae bowed. Female: Pronotal edges slightly converging anteriorly, fore spur narrower, fore tibiae nearly straight, hind legs normal.

Type. — Luquillo Forest, Puerto Rico. USNM.

Remarks. — This species has been consistently mis-named histeroides Harold in all recent literature since Chapin (1934). The type of Canthon histeroides Harold in the Paris Museum was recently examined by the author and found to be quite different from the Puerto Rican species now described as new. For a discussion of the geographical variation and distribution of this species (under the name histeroides) see Matthews (1965), and for a description of the immature stages see Matthews (1963).

Material examined. — 1,043 specimens. Paratypes are deposited in AM, ANSP, BMNH, CNC, GH, MNHN, USNM.

PUERTO RICO. 69 localities throughout the island, 24 March 1962 to 5 March 1964, E. G. Matthews (1,041); Ponce, Wersching Finca, 23 January 1934, R. G. Oakley (1), [USNM]; Aibonito, Díaz Finca, 4 September 1934, R. G. Oakley (1), [USNM].

Genus CANTHONELLA Chapin

Canthonella Chapin, 1930, American Mus. Nov. No. 409, 2 pp; Chapin, 1935, Proc. Biol. Soc. Washington, vol. 47, p. 101; Blackwelder, 1944, United States Nat. Mus. Bull. 185, p. 198; Wolcott, 1948, J. Agr. Univ. Puerto Rico, vol. 32, p. 247; Martínez, 1954, Natura, vol. 1, p. 64; Pereira and Martínez, 1956, Rev. Brasileira Ent., vol. 6, p. 99; Matthews, 1963, Col. Bull., vol. 17, p. 110; Pereira and Martínez,

1963, Acta Zool. Mexicana, vol. 6, p. 2; Matthews, 1965, Trans. American Ent. Soc., vol. 91, p. 447; Zayas and Matthews, 1966, Poeyana, Ser. A, No. 14, p. 16.

Type of genus. — Canthonella parva Chapin, 1930.

Description. — Small beetles (1.7-3.5 mm long), entirely densely punctate, each puncture bearing a long, fine recumbent white seta. Elytra with subhumeral pale markings. Clypeus bidentate, the teeth acute, approximated, separated by a U-shaped emargination. Dorsal ocular areas separated by a distance equal to 10-12 times their width. Posterior edge of head not carinate Antennae nine-segmented (fig. 90). Labium semi-oval, not or margined. appreciably emarginate apically, labial palpi with second segment the largest (figs. 84, 85). Pronotum completely margined basally. Anterior part of prothorax below deeply excavated, the excavations bounded posteriorly by a vertical wall and strong margin. Mesosternum only three to four times as wide as long. Meso-metasternal suture very feebly angulate or evenly arcuate (fig. 86). Mid-coxal cavities somewhat oblique, their inner margins narrow. Elytra with eight distinct striae, the seventh effaced anteriorly. No lateral elytral carina. Fore tibia with outer teeth unusually small, rest of margin serrate. Fore spur long, acute, curved down in both sexes. Femora densely, finely punctate and pilose. Middle and hind tibiae very slender, tapering at apex, the spurs very small. Tarsi long, the segments cylindrical, first segment of hind tarsi much shorter than second (fig. 95). Tarsal claws with a strong basal tooth (fig. 94). Abdominal sternites with a row of large, close-set punctures along basal edge, except on first and sixth sternite. Sixth sternite much longer than others, as long as previous two or three sternites combined. Pygidium with strong basal margin. Aedeagus very elongated, with parameres very slender, strongly bent at right angle to basal piece, with apical portion of internal sac protruding between parameres. Base of basal piece with bottleneck (figs. 91-93). No sexual dimorphism.

Distribution. — Cuba, Hispaniola, Puerto Rico. Recorded here for the first time from Hispaniola.

Remarks. — Canthonella is taxonomically the most isolated genus of canthonines in the Western Hemisphere. Attempts have been made to group it with Ipselissus Olsoufieff of South America (Martínez, 1954; Pereira and Martínez, 1963; Pereira, in litt.), but these authors conclude that the two genera are not very close, sharing principally the dentate tarsal claws — a feature which by itself cannot be considered decisive. As in the case of Canthochilum, the male genitalia will provide the most important clues to relationships, being of a very unusual form in Canthonella (figs. 91-93), but the genitalia of most of the small canthonine genera have not been examined. There can be no doubt that Canthonella belongs with the

host of small canthonines now largely confined to the barrier-limited Old World tropics, but also including New World elements such as *Canthochilum, Ipselissus*, and *Zonocopris*. However, *Canthonella* cannot be closely grouped with the latter three genera, in the author's opinion, as it does not show the primitive features (morphological or behavioral) which place these genera between the subtribes Canthonina and Dichotomina (see remarks under *Canthochilum*). *Canthonella* is clearly a canthonine, as is shown by its slender, distally narrowed tibiae (fig. 86). The Puerto Rican species (*parva* Chapin) is a very accomplished ball roller, and in its rolling position resembles some of the known Old World ball rollers (Matthews, 1965).

The author believes that when a thorough study is finally made, *Canthonella* will be found to have its closest relatives in the region of the Indian Ocean or the Australian Region, among the numerous canthonine genera which are largely confined to islands. The Old World material is unfortunately very scarce in collections, as no one there has carried out the sort of systematic trapping done in recent years by various workers in the Neotropical Region.

Until now only two species of *Canthonella* were known (erroneously synonymized under one name by Martínez, 1954), but the author's collecting in the Dominican Republic has now added two more. The discovery of two species on Hispaniola after only a very brief collecting period, while after years of thorough collecting in Cuba and Puerto Rico only one species continues to be known from each of those islands, raises the distinct possibility that there are more undiscovered *Canthonella* on Hispaniola.

Key to the Species of Canthonella

- 3(2'). Eighth elytral stria, along epipleural carina, not more strongly punctate than remaining striae; pale area of elytron limited to fourth interval outward, white or very pale yellow. Cuba pygmaea (Harold).
- 3'. Eighth elytral stria marked by deep punctures, much stronger than those of remaining striae; pale area of elytron invading third interval, yellow-orange in color. Hispaniola isabellae n. sp.

Canthonella pygmaea (Harold)

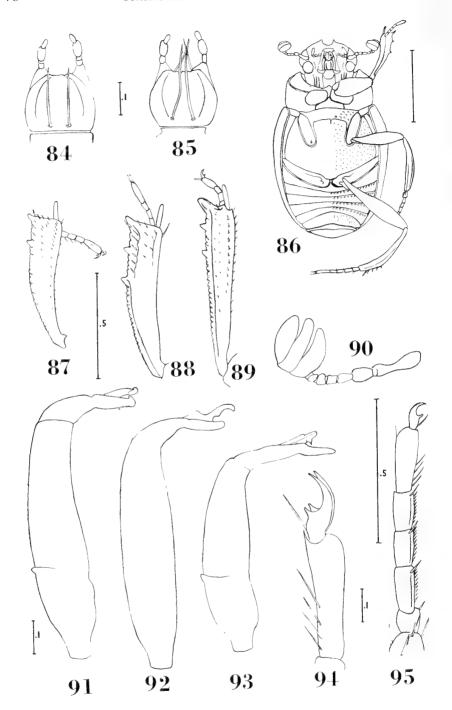
Canthon pygmaeus Harold, 1869, Col. Hefte, vol. 5, p. 96; Leng and Mutchler, 1914, Bull. American Mus. Nat. His., vol. 33, p. 438; Balthasar, 1939, Fol. Zool. Hydrobiol., vol. 9, p. 207.

Canthonella pygmaea (Harold), Chapin, 1930, American Mus. Nov. No. 409, p. 2; Blackwelder, 1944, United States Nat. Mus. Bull. 185, p. 198; Martínez, 1954, Natura, vol. 1, p. 64; Pereira and Martínez, 1956, Rev. Brasileira Ent., vol. 6, p. 99; Zayas and Matthews, 1966, Poeyana, Ser. A, No. 14, p. 16.

Description. — Oval, strongly convex, finely pilose, body shiny black except for large subhumeral white patches on elytra, legs fuscous. Dorsal ocular areas separated by a distance equal to 10 times their width at base. Labium rounded, without apical emargination, palpi with second segment larger than first, third segment very small (fig. 84). Base of mentum bearing two very long setae directed forward. Pronotum distinctly narrower than elytral bases, the latter 1.3 times as wide as pronotum at widest point. Pronotum with lateral edges slightly converging anteriorly for basal two thirds, then abruptly bending inward at an obtuse angle for anterior third. All elytral striae shallow, impunctate, consisting of two very fine parallel lines close together. Interstriae flat, none more raised than others, extremely finely punctate and pilose. All intervals from fourth outward and epipleura very pale yellow (probably white in life) for anterior fourth of elytral length, the pale areas not quite reaching elytral base (fig. 96). Legs proportionately short (fig. 96). Fore tibia broad and transversely truncate apically, with two very small outer teeth distally, the rest of outer margin finely serrulate (fig. 87). Aedeagus as in fig. 91. Total length 2.5-3.0 mm.

Type. — Cuba. Lost.

Remarks. — Correct identification of this species has become complicated by the facts that the original type of Harold is not in the Paris Museum (Descarpentries, in litt.) and that a specimen is present in the Humboldt University museum in Berlin. It was sent to the author through the courtesy of Dr. F. Hieke. This specimen would normally be considered the type, but on examination by the author it proved to belong to the Puerto Rican species. Zayas and



Matthews (1966), in discussing this problem, note that the Berlin specimen cannot be accepted as the type of *Canthon pygmaeus* Harold because of discrepancies with the original description. In particular, the original description specifies that the fore tibiae are bidentate and that the habitat is Cuba, while the Berlin specimen has the tibiae tridentate and is clearly labelled "Portorico."

Ecology. — Poorly known. Zayas has collected it in leaf litter at various locations and altitudes in Cuba, indicating that the species may be eurytopic.

Distribution. — Cuba. It is reported from Cueva del Indio, Havana Province (Martínez, 1954) and the plateau of Las Mulas in the Sierra de Cristal, Oriente Province (Zayas and Matthews, 1966) in addition to the locality cited below.

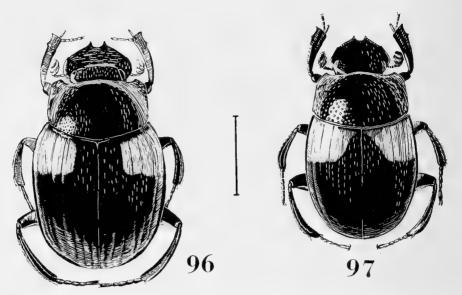
Material examined. — Four specimens.

CUBA. *Pinar del Río:* El Pinar, Los Palacios, July 1956, F. de Zayas (4), [USNM].

Canthonella isabellae n. sp.

Description. — Oval, strongly convex, finely pilose, body shiny black except for large humeral orange-yellow patches on elytra, legs piceous. Dorsal ocular areas separated by a distance equal to 10 times their width at base. Labium rounded, without apical emargination, palpi of second segment larger than first, third segment very small. Base of mentum bearing two very long setae directed forward. Pronotum only a little narrower than elytral bases, the elytra 1.2 times as wide as pronotum at widest point (fig. 97). Posterior margin of pronotum extremely fine. Pronotum with lateral edges slightly converging anteriorly for basal two thirds, then abruptly bending inward at an obtuse angle for anterior third. Eighth elytral stria strongly, deeply punctate, the punctures large and well separated. Seventh stria subpunctate and very wide and shallow. Remaining striae impunctate, consisting of two fine parallel lines close together. Interstriae flat, none more raised than others, extremely finely punctate and

Figures 84-95. Fig. 84, Canthonella pygmaea (Harold), labium. Fig. 85, Canthonella constans n. sp., labium. Fig. 86, Canthonella constans n. sp., ventral view. Fig. 87, Canthonella pygmaea (Harold), left front tibia and tarsus. Fig. 88, Canthonella constans n. sp., left front tibia and tarsus. Fig. 89, Canthonella parva Chapin, left front tibia and tarsus. Fig. 90, Canthonella constans n. sp., antenna. Fig. 91, Canthonella pygmaea (Harold), aedeagus. Fig. 92, Canthonella constans n. sp., aedeagus. Fig. 93, Canthonella parva Chapin, aedeagus. Fig. 94, Canthonella constans n. sp., last segment and claws of hind tarsus. Fig. 95, Canthonella constans n. sp., hind tarsus.



Figures 96-97. Fig. 96, Canthonella pygmaea (Harold). Fig. 97, Canthonella isabellae n. sp., holotype.

pilose. Pale patches on elytra orange-yellow, invading third elytral intervals and, very faintly, second and first as well, covering basal quarter of remaining intervals and epipleura, and extending right up to bases of elytra (fig. 97). Legs proportionately short (fig. 97). Fore tibia broad and transversely truncate apically, with two very small outer teeth distally, the rest of outer margin finely serrulate. Total length 2.5 mm.

Type. — 31 km northwest of Santo Domingo, Dominican Republic. USNM.

Remarks. — This species is closely related to the Cuban *pygmaea* Harold but may be told by the characters mentioned in the key and its relatively narrower hind body.

Ecology. — Evidently inhabits leaf litter in lowland mesophytic forests, which are almost wholly destroyed, at least in the southern Dominican Republic where the author collected. The single known specimen came to a trap baited with cow dung.

Distribution. — Hispaniola.

Material examined. — Unique holotype.

HISPANIOLA. DOMINICAN REPUBLIC. *Distrito Nacional:* 31 km NW of Santo Domingo on Santiago Highway (Carretera Duarte), 150 ft, 14 October 1964, E. G. Matthews (1), [USNM].

Canthonella constans n. sp.

Description. — Oval, somewhat flattened, finely pilose, entirely fuscous, elytra a little lighter except along suture, with two pale yellow spots on each elytron on fifth and seventh intervals and epipleura near base, sometimes an additional smaller spot between others on sixth interval. Legs fuscous. Dorsal ocular areas separated by a distance equal to 12 times their width at base. Labium with very shallow, arcuate emargination (fig. 85), palpi with second segment larger than first, third segment very small. Pronotum distinctly narrower than elytra, the latter 1.3 times as wide as pronotum at widest point. Lateral edges of pronotum subparallel for basal two thirds, abruptly bending inward at an obtuse angle at anterior third. All elytral striae impunctate, shallow, consisting of two very fine parallel lines close together. Interstriae flat, none more raised than others, extremely finely punctate and pilose. Epipleura, seventh, fifth, and sometimes sixth intervals with basal pale areas as described above (fig. 98). Legs proportionately long and slender (fig. 98). Fore tibia transversely truncate apically, with three small, acute outer teeth, the distal one slightly oblique (fig. 88). Outer tibial margin finely serrulate between teeth. Aedeagus as in fig. 92. Total length 2.2-2.6 mm.

Type. — 11 km south of Constanza, Dominican Republic. USNM.

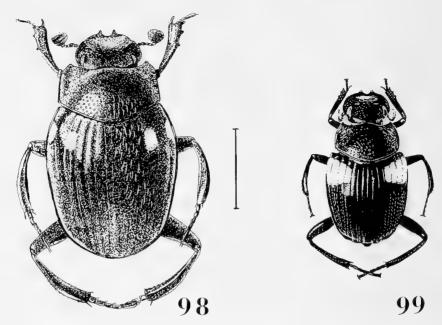
Remarks. — This species is easily recognizable by its relatively pale overall coloring and the fact that the elytral pale patches are broken up into separate spots. Its relatively long legs and number of teeth of the fore tibia bring it closer to the Puerto Rican parva Chapin than to the other species.

Ecology. — This is evidently a high-altitude species and comes second only to Canthochilum guayca Zayas and Matthews of Cuba as an altitude record holder for the subfamily in the Antilles. It is fully winged, however. It was found on the edges of a recently destroyed pine forest in the Cordillera Central, in leaf litter. All specimens were collected in traps baited with human excrement.

Distribution. — Hispaniola.

Material examined. — Eight specimens. Paratypes are deposited in BMNH, MNHN, USNM.

HISPANIOLA. DOMINICAN REPUBLIC. *La Vega*: 11 km S of Constanza on road to San José de Ocoa, Cordillera Central, 5,700 ft, 14 October 1964, E. G. Matthews (8).



Figures 98-99. Fig. 98, Canthonella constans n. sp., holotype. Fig. 99, Canthonella parva (Chapin).

Canthonella parva Chapin

Canthonella parva Chapin, 1930, American Mus. Nov. No. 409, 2 pp; Chapin, 1934, Proc. Biol. Soc. Washington, vol. 47, p. 101; Blackwelder, 1944, United States Nat. Mus. Bull. 185, p. 198; Wolcott, 1948, J. Agr. Univ. Puerto Rico, vol. 32, p. 247; Matthews, 1965, Trans. American Ent. Soc., vol. 91, p. 448.

Canthonella pygmaea Martínez, 1954 (nec Harold, 1869), Natura, vol. 1, p. 64; Pereira and Martínez, 1956, Rev. Brasileira Ent., vol. 6, p. 99; Matthews, 1963, Col. Bull., vol. 17, p. 110.

Description. — Narrowly oval, moderately convex, finely pilose, body shiny black except for large subhumeral white patches on elytra, legs black. Dorsal ocular areas separated by a distance equal to 10 times their width at base. Labium rounded, apically truncate, palpi with second segment larger than first, third segment very small. Base of mentum with two very long setae directed forward. Pronotum distinctly narrower than elytra, the latter 1.3 times as wide as pronotum at widest point. Pronotum with lateral edges evenly curved (fig. 99). Elytra deeply striate. Third interstria with three merging callosities at beginning of posterior declivity and one callosity terminally. Fifth interstria with one or two callosities at beginning of posterior declivity. First, third, and fifth interstriae posteriorly more raised than others. Seventh stria

posteriorly more depressed than others, forming a posterior transverse depression on elytra. All intervals from fourth outward and epipleura white for basal one quarter of elytral length, the white areas not quite reaching elytral base (fig. 99). Legs proportionately very long (fig. 99). Fore tibia straight, only slightly expanding from base to apex, the outer edge very finely serrulate, distally with three teeth, the proximal two very small, the distal one long and acute, directed obliquely forward and downward (fig. 89). Aedeagus as in fig. 93. Total length 1.7-3.0 mm.

Type. — Coamo Springs, Puerto Rico. American Museum of Natural History No. 28456.

Remarks. — The ecological distribution, geographical variation, and feeding habits of this species are discussed by Matthews (1965). Two subspecies are recognized on the basis of ecological distribution and size: the nominotypical one found throughout the low altitude belt of Puerto Rico, and *C. parva luquillensis* Matthews, found in the Luquillo Range at moderate altitudes.

The synonymization of this species with *C. pygmaea* (Harold) by Martínez (1954) was apparently based on specimens of *pygmaea* erroneously labelled from Puerto Rico (Las Marías). The two species were again separated by Matthews (1965).

Ecology. — This is a leaf-litter species, confined to forests and dense scrub, a euryphagous coprophage, diurnal in its activity, and a very adept ball roller (see Matthews, 1965, for details).

Distribution. — Puerto Rico. The following new material has been examined since the 169 specimens reported in Matthews (1965): Luquillo Forest, El Yunque Biol. Sta., 2,100 ft, Paul and Phyllis Spangler (5), [USNM]; Luquillo Forest, Rt. 191, km 9.7, 16 August 1961, O. S. Flint and P. Spangler (6), [USNM]; Maricao Forest, 2,000 ft, 9-13 January 1961, A. B. Gurney (3), [USNM]; no further data: No. 26418, Portorico Moritz (1), [ZMHU].

Genus PSEUDOCANTHON Bates

Pseudocanthon Bates, 1887, Biologia Centrali Americana, Coleoptera vol. 2, pt. 2, p. 35.

Opiocanthon Paulian, 1947, Coléoptères des Antilles, vol. 1, p. 30. New synonymy.

Type of genus. — Canthon perplexus Leconte, 1847; of Opiocanthon: Canthon vitraci Fleutiaux and Sallé, 1889.

Description. — Small beetles (3.5-6.5 mm in length), uniformly dark with

the legs usually paler. Clypeus with four approximated, rounded teeth, the middle ones much larger. A slight angulation of head margin at clypeogenal suture. Dorsal ocular areas moderate to large, separated by a distance equal to 5-7 times their width at base. Posterior edge of head not carinate or margined. Labium wider than long, deeply emarginate, the palpi with basal segment the largest (figs. 100-102). Pronotum not margined basally. Lateral edges of pronotum appearing straight and subparallel basally when viewed from above. Anterior part of prothorax below excavated, the excavation bounded posteriorly by a transverse margin. Mesosternum relatively long, only 5-8 times as wide as long. Meso-metasternal suture feebly arcuate. Inner edge of midcoxal cavities narrowly margined. Elytra with nine striae, sometimes obsolete, striae 5 and 6 approximated basally, stria 7 effaced anteriorly. Stria 8 present as an incomplete segment near elytral base, often entirely effaced. Epipleura broad. Surfaces of elytra densely and evenly provided with very short setae, visible in oblique light and at high magnification. Anterior tibiae with apex transversely sinuate, the outer edge with three prominent teeth, the inner edge distinctly bent in at about middle, sometimes expanded here. Ventral surface of hind femur with a fine margin paralleling anterior edge (except in sylvaticus). Middle and hind tarsal segments triangular, first segment of hind tarsus subequal to second or slightly longer. Tarsal claws with a basal angulate expansion, giving them a subdentate appearance (figs. 105, 106). Abdominal sternites impunctate. Pygidium with or without a basal carina separating it from propygidium. Pygidium not projecting beyond elytral edges in dorsal view. Male parameres normal, long, with prominent rounded ventral projection (figs. 107, 108).

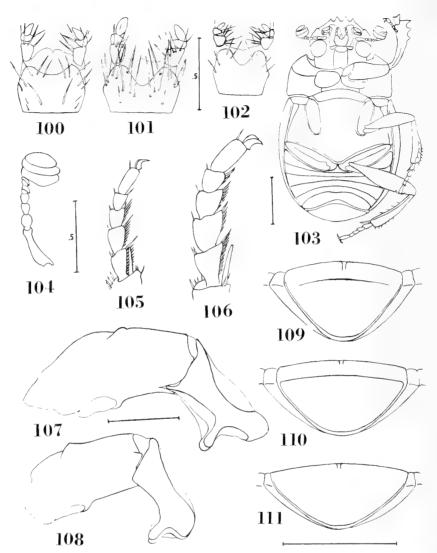
Distribution. — The Neotropical Region (one species entering the southern United States). Three species on the continent, one of which enters the Lesser Antilles (Grenada, Grenadines). Five species and one subspecies exclusive to the Antilles: Jamaica, St. Lucia, Dominica, and Guadeloupe, from which islands the genus is here recorded for the first time.

Remarks. — Arrow (1903) first recorded this genus from the Antilles (Ps. chlorizans Bates from Mustique and Union). It is therefore puzzling that Pereira and Martínez (1956) should state that Pseudocanthon does not occur in the region. Actually, with the discovery of four new Antillean species by the present author, plus the inclusion of Canthon vitraci Fleutiaux and Sallé in the genus, Pseudocanthon is seen to be essentially an Antillean genus today.

In his original description Bates (1887) characterized the genus by its long mesosternum, inwardly sinuate anterior tibiae, and deflexed pygidium. In 1889 Bates added the features of the basally parallel lateral edges of the pronotum and the elytra being studded with minute hair-scales. Arrow (1903) emphasizes the angulate inner edge of the fore tibiae as a generic character. Martínez (1947) emphasizes the parallel-sided form and adds new features of the labium and labial palpi. Halffter (1961) points out that the labial features are not clearly separable from those of *Canthon*, and concludes that the only precise character that separates *Pseudocanthon* from *Canthon* is the absence in the former of a basal carina or margin on the pygidium. Unfortunately, all the Antillean species discovered by the present author have this carina clearly marked.

In spite of the disagreement among specialists as to which features are of generic importance, there can be no doubt that Pseudocanthon is a valid genus, with an unmistakable facies. The fact that the subparallel pronotal sides are due to an "optical effect" (Arrow, 1903), or to the position of the median angles of the lateral margin (Halffter, 1961), does not change the fact that the pronotum does seem parallel-sided (or nearly so) in direct dorsal view in Pseudocanthon, while it does not seem so in Canthon (compare figs. 124-128 with 130 and 141-143). It is necessary to consider this and a number of additional features as a whole, not singly, to arrive at a characterization of the genus. Among these features are the excavated (not merely carinate) propleurae, unmargined hind edge of the head, and all the features previously pointed out by Bates and Arrow. The form of the aedeagus is remarkably constant in all the species examined by the author (only Ps. xanthurus [Blanchard] was not examined), but is not exclusive to the genus. One of the key characters given by Pereira and Martínez (1956) — the first two hind tarsal segments being subequal - does not hold for the Antillean species, whose first tarsal segment may be subequal or distinctly longer (iuanalaoi) than the second segment.

Opiocanthon Paulian (1947) was established on the basis of the Guadalupan species vitraci Fleutiaux and Sallé. The features used by Paulian to characterize the genus were so general that it proved impossible for later workers (Pereira and Martínez, 1956) to recognize it without having seen the type species. When the species was re-collected and examined by the present author, it became clear that Opiocanthon has no validity as a generic category.



Figures 100-111. Fig. 100, Pseudocanthon sylvaticus n. sp., labium. Fig. 101, Pseudocanthon vitraci (Fleutiaux and Sallé), labium. Fig. 102, Pseudocanthon jamaicensis n. sp., labium. Fig. 103, Pseudocanthon jamaicensis n. sp., ventral view. Fig. 104, Pseudocanthon jamaicensis n. sp., antenna. Fig. 105, Pseudocanthon jamaicensis n. sp., hind tarsus. Fig. 106, Pseudocanthon vitraci (Fleutiaux and Sallé), hind tarsus. Fig. 107, Pseudocanthon vitraci (Fleutiaux and Sallé), aedeagus. Fig. 108, Pseudocanthon jamaicensis n. sp., aedeagus. Fig. 109, Pseudocanthon caeranus n. sp., pygidium. Fig. 110, Pseudocanthon vitraci (Fleutiaux and Sallé), pygidium. Fig. 111, Pseudocanthon chlorizans (Bates), pygidium.

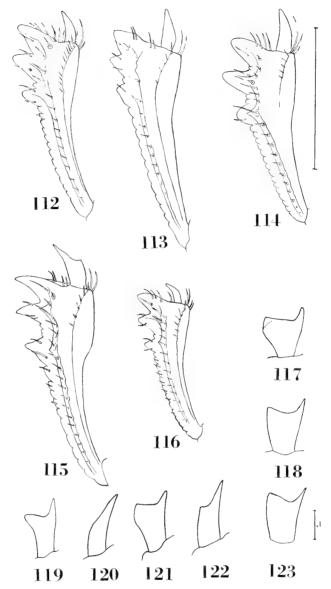
Key to the Species of Pseudocanthon of the Antilles

1.	Base of pygidium with no trace of any carina separating it from pro pygidium (fig. 111). Grenada, Grenadines chlorizans (Bates)
1'.	Base of pygidium with a distinct carina paralleling distal edges of elytra in repose (figs. 109, 110)
2(1').	Pronotum evenly, densely, and coarsely punctate; elytral striae distinct body surfaces shiny or with distinct alutaceous sheen and usually with greenish reflections; dorsal ocular areas small, separated by a distance equal to 7-8 times their width
2'.	Pronotum entirely impunctate or unevenly punctate with the puncturer concentrated anteriorly; elytral striae indistinct or obsolescent; body surfaces densely shagreened, dull, never with greenish reflections ocular areas large, separated by a distance equal to five times their width
3(2).	Total length 4.8-6.2 mm; rotund (fig. 125); minute elytral setae difficul to see. St. Lucia iuanalaoi n. sp
3'.	Total length 3.5-4.7 mm; broadly oblong (fig. 127); minute elytral setae distinct. Jamaica jamaicensis n. sp
4(2').	Ventral surface of hind femur without a fine carina paralleling anterior edge; teeth of fore tibiae not prominent (fig. 113); proximal latera margins of pronotum subparallel, slightly diverging anteriorly in make (fig. 128); metasternum impunctate. Dominica sylvaticus n. sp
4'.	Ventral surface of hind femur with a fine margin closely paralleling an terior edge; teeth of fore tibiae prominent; proximal lateral marging of pronotum converging anteriorly; metasternum punctate
5(4').	Inner edge of fore tibia strongly expanded opposite outer teeth (fig 115); head and pronotum very finely punctate, the punctures sparse and barely visible; minute setae of elytra clearly visible in oblique light; legs pale, contrasting with dark body color; base of pygidium completely margined (fig. 110). Guadeloupe
5'.	Inner edge of fore tibia not appreciably expanded (fig. 114); head and anterior part of pronotum rather densely punctate, the punctures shallow but clearly visible; minute setae of elytra very difficult to see legs dark; base of pygidium incompletely margined laterally (fig. 109)

Pseudocanthon chlorizans (Bates)

Canthon chlorizans Bates, 1887, Biologia Centrali Americana, Coleoptera, vol. 2, pt. 2, p. 34.

Pseudocanthon chlorizans (Bates), Bates, 1889, Biologia Centrali Americana, Coleoptera, vol. 2, pt. 2, suppl. p. 386; Arrow, 1903, Trans. Ent. Soc. London 1903, pt. 4, p. 510.



Figures 112-123. Fig. 112, Pseudocanthon chlorizans (Bates), \Im , left front tibia. Fig. 113, Pseudocanthon sylvaticus n. sp., \Im , left front tibia. Fig. 114, Pseudocanthon caeranus n. sp., \Im , left front tibia. Fig. 115, Pseudocanthon vitraci (Fleutiaux and Sallé), \Im , left front tibia. Fig. 116, Pseudocanthon j. jamaicensis n. sp., \Im , left front tibia. Fig. 117, Pseudocanthon sylvaticus n. sp., \Im , right fore spur. Fig. 118, Pseudocanthon caeranus n. sp., \Im , right

Description. — Oblong-oval, black, shiny, the legs rufous, antennal clubs yellow. Head surface shiny, densely, evenly, and shallowly punctate, the interpunctural surface finely shagreened. Ocular areas moderate, the distance between them equal to seven times their maximum width. Pronotal surface shiny, moderately densely and evenly punctate, the surface between punctures smooth. Median lobe of metasternum densely punctate. Elytral striae distinct but impunctate and superficial. Intervals flat, shiny, smooth, and extremely finely and sparsely punctate, each puncture bearing a very short seta. Anterior tibiae with three large outer distal teeth prominent, inner margin bent inward at about mid point (fig. 112). Inner longitudinal carina of fore tibia complete. Femora very finely punctate with short setae. Middle and hind femora with a fine margin paralleling anterior border on ventral surface. Tarsal segments triangular. First segment of hind tarsus distinctly longer than second. Pygidium basally without any margin separating it from propygidium. Pygidial disc densely but very finely and shallowly punctate, smooth. Total length 3.7-5.5 mm.

Sexual dimorphism. — Male: Fore spur long and relatively narrow, apically bifurcate, the two teeth approximately equal in size. Last abdominal sternite shortened medially. Female: Fore spur evenly tapering to a point. Last abdominal sternite not shortened medially.

Type. — Juquila, Oaxaca. BMNH.

Remarks. — This species is immediately separable from all other Pseudocanthon of the Antilles by the absence of a basal carina on the pygidium. The Antillean specimens are more finely punctate, shinier, and less greenish than the Mexican ones. Arrow (1903) was the first to record this species, and the genus, from the Antilles on the basis of H. H. Smith's specimens from the Grenadines (also examined by the present author).

Ecology. — In Grenada and Bequia this species is confined to low-land xerophytic forest and scrub. It was not collected in moist forest, in open pastures, or at any altitude above sea level. The species appears to be far more common on Bequia than on Grenada. It comes to cow dung and human excrement, not to carrion.

Distribution. — Ps. chlorizans is presently known only from Mexico, Grenada, and the Grenadines, but the continental areas in between have been very poorly collected. It is here recorded for the first time from Grenada.

fore spur. Fig. 119, Pseudocanthon j. jamaicensis n. sp., δ , right fore spur. Fig. 120, Pseudocanthon j. jamaicensis n. sp., φ , right fore spur. Fig. 121, Pseudocanthon j. viridescens n. subsp., δ , right fore spur. Fig. 122, Pseudocanthon j. viridescens n. subsp., φ , right fore spur. Fig. 123, Pseudocanthon vitraci (Fleutiaux and Sallé), δ , right fore spur.

Material examined. — 24 specimens. The author's material is deposited in BMNH, MNHN, and USNM.

GRENADA. St. George Parish: Grande Anse, 4 mi S of St. George's, sea level, 9 July 1965, E. G. Matthews (4); St. David Parish: Westerhall Estate, sea level, 9 July 1965, E. G. Matthews (1).

GRENADINES. UNION: H. H. Smith (1), [BMNH]; MUSTIQUE: H. H. Smith (1), [BMNH]; BEQUIA: 13 July 1965, E. G. Matthews (12); CARRIACOU: Sta. 143, 144, 17 January 1936, R. E. Blackwelder (5), [USNM].

Pseudocanthon iuanalaoi n. sp.

Description. — Broadly oval, black with greenish tinge, alutaceous, with legs and antennae rufous. Head surface densely and moderately coarsely punctate, shagreened between punctures. Dorsal ocular areas small, separated by a distance equal to eight times their width at base. Pronotal surface very densely, evenly, and coarsely punctate, the punctures separated by distances equal to 1-2 times their diameter. Interpunctural surface finely shagreened, giving the whole an alutaceous sheen. Median lobe of metasternum densely punctate. Elytral striae distinct, impunctate, not impressed, consisting of fine parallel double lines. Intervals flat, very finely shagreened, alutaceous, extremely finely punctate, each puncture bearing a very minute seta, difficult to see. Fore tibia with outer distal teeth prominent. Inner margin moderately expanded inwardly opposite outer teeth, forming a mild angulation, slightly more accentuated in male. Inner longitudinal carina of dorsal surface of tibia complete. Femora extremely finely punctate. Ventral surface of hind femur with very fine margin paralleling and close to anterior edge. Middle and hind tarsal segments subtriangular, first segment of hind tarsus distinctly longer than second. Pygidium with a complete basal margin separating it from propygidium, this margin-becoming very fine at lateral ends. Pygidial disc shagreened and very finely punctate. Total length 4.8-6.2 mm.

Sexual dimorphism. — Male: Fore spur expanded distally, bifurcate with the outer tooth much more acute, as in vitraci and caeranus (fig. 123). Last abdominal sternite shortened medially. Female: Fore spur tapering evenly to a single point. Last abdominal sternite not shortened medially.

Type. — Union Agricultural Station, St. Lucia. USNM.

Remarks. — The nearest relative of this species is Ps. jamaicensis n. sp. of Jamaica, from which it differs only in size, in its more rounded shape (fig. 125), and in the shape of the male fore spur. Both these species probably represent descendants of the same (now

extinct) ancestral species which invaded Jamaica on the one hand, and the Lesser Antilles on the other, from the continent. In the Lesser Antilles *Ps. iuanalaoi* may be easily told from *Ps. chlorizans* to the south by the presence of a basal carina on the pygidium, its larger size, surface shagreening, greenish tinge, etc., and from the other three species to the north by its dense and coarse punctuation, greenish tinge, relative glossiness, and small ocular areas.

Ecology. — This species is extraordinarily abundant in all low-land forest areas of St. Lucia, both dry and moist. The trapping yield in the entire area surveyed was 15.1 specimens per trap, with a maximum of 73 specimens in one trap near the Union Agricultural Station. It becomes markedly less abundant in the highland humid forests and coffee groves of the interior. Unlike any other species of Pseudocanthon encountered, it may occasionally be found under cow dung in open pastures (three specimens having been collected in this manner). This may be the result of two factors: the high population densities in the forests, causing an "overflow" into pastures, and the complete absence of any true pasture-inhabiting Scarabaeinae on St. Lucia, unlike any of the neighboring islands. Ps. iuanalaoi comes to cow dung traps, but in much greater numbers to human excrement.

Distribution. — St. Lucia.

Material examined. — 243 specimens. Paratypes are deposited in AM, ANSP, BMNH, CNC, GH, MNHN, USNM.

ST. LUCIA. *Quarter of Castries:* Gros Morne, 2 mi SE of Castries, 1,000 ft, 15 July 1965, E. G. Matthews (29); 2 mi N of Castries, sea level, 16 July 1965, E. G. Matthews (58); 2 mi S of Cul de Sac River on Soufrière road, 300 ft, 16 July 1965, E. G. Matthews (16); Barre de l'Ile, 800 ft, 16 July 1965, E. G. Matthews (4); Jct. Millette and Roseau Rivers, Sta. 207, 29 March 1936, R. E. Blackwelder (1), [USNM]; *Quarter of Dennery:* Morne Vent, 2 mi N of Dennery, sea level, 16 July 1965, E. G. Matthews (21); *Quarter of Gros Ilet:* Union Agricultural Station, 200 ft, 16 July 1965, E. G. Matthews (114).

Pseudocanthon sylvaticus n. sp.

Description. — Oblong, flattened, entirely sericeous, fulvous to fuscous, legs and antennae pale rufous. Head surface impunctate, finely shagreened. Ocular areas large, separated by a distance equal to five times their width at

base. Pronotal surface appearing entirely impunctate at all but the highest magnifications, finely shagreened, giving the whole a dull, silky sheen. Metasternum impunctate. Elytral striae indistinct, impunctate. Striae 1 and 7 more impressed than others near base, the latter accentuating the humeral callus (fig. 128). Intervals flat, extremely finely punctate, appearing impunctate at all but the highest magnifications, finely shagreened, giving the whole a dull, silky sheen. Intervals with a few very short setae, clear only in teneral specimens. Fore tibiae with the outer distal teeth triangular, not prominent, with inner margin curved inward, with only a slight trace of an expansion opposite outer teeth (fig. 113). Inner longitudinal carina of dorsal surface of tibia complete. Femora impunctate, anterior edge of hind femur not margined. Tarsal segments triangular, first segment of hind tarsus equal in length to second. Pygidium with a complete basal carina. Pygidial disc shagreened, impunctate. Total length 5.5-6.5 mm.

Sexual dimorphism. — Male: Fore spur strongly expanded and bifurcate, the outer prong acute, the inner one very broad (fig. 117). Lateral edges of pronotum parallel basally or anteriorly diverging slightly (fig. 128). Last abdominal sternite shortened medially. Female: Fore spur tapering and acute (fig. 113). Lateral edges of pronotum parallel or slightly converging anteriorly. Last abdominal sternite not shortened medially.

Type. — Morne Micotrin, Dominica. USNM.

Remarks. — The sexual dimorphism in the shape of the prothorax, the absence of a margin along the anterior edge of the hind femur, and the complete absence of distinct punctuation are unique features of this species within the genus Pseudocanthon.

Ecology. — Ps. sylvaticus is one of the only two species of Scarabaeinae known from the Lesser Antilles adapted to live in the highland humid forests. Its altitude range is 1,400 to 2,800 ft (undoubtedly higher, as this is as high as the author could go) and its distribution thus coincides with that of the rain forest and montane thicket (Hodge, 1954). It is probably nocturnal in its activity, as a specimen was caught walking at night by Dr. O. S. Flint (the species is not attracted to light). Two specimens were collected under cow dung at the edge of the forest, but this experience was not repeated in spite of continued searching. All other specimens were collected in jar traps baited with cow dung. None came to carrion.

Distribution. — Dominica.

Material examined. — 31 specimens. Paratypes are deposited in AM, BMNH, CNC, GH, MNHN, USNM.

DOMINICA. St. Paul Parish: 1.6 mi NW of Pont Cassé, 1,400 ft, 24-25 May 1964, E. G. Matthews and O. S. Flint (5); .4 mi E

of Pont Cassé, 2,000 ft, 27 April 1964, O. S. Flint (1), [USNM]; 25 May 1964, E. G. Matthews and O. S. Flint (4); *St. David Parish:* Castle Bruce Junction (2.5 mi E of Pont Cassé on Rosalie Rd.), 1,600 ft, 25 May 1964, E. G. Matthews and O. S. Flint (2); *St. George Parish:* Morne Micotrin (M. Macaque) along road to L'Etang (Fresh Water Lake), 2,700-2,800 ft, 28 May 1964, E. G. Matthews and O. S. Flint (19).

Pseudocanthon caeranus n. sp.

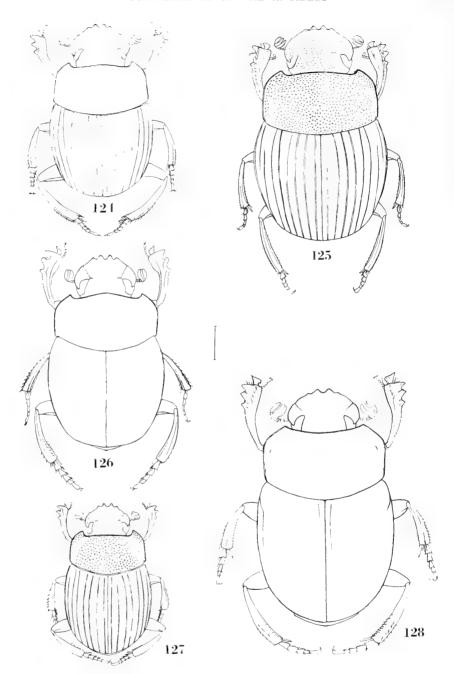
Description. — Broadly oval, black, sericeous, with legs dark rufous, antennae paler. Head surface densely and coarsely but shallowly punctate and shagreened. Dorsal ocular areas large, separated by a distance equal to 51/2 times their width at base. Pronotal surface densely and coarsely punctate on anterior and lateral portions, finely punctate on disc. Surface between punctures shagreened, giving the whole a dull, silky sheen. Median lobe of metasternum finely punctate. Elytral striae indistinct, impunctate. Intervals flat, distinctly shagreened, giving surface a silky sheen, and very finely punctate, each puncture bearing an extremely short seta, all but invisible. Fore tibia with outer distal teeth prominent, the inner margin slightly angulate at about middle (fig. 114). Inner longitudinal carina of upper surface of tibia incomplete (fig. 114). Femora extremely finely punctate, anterior edge of hind femur margined. Tarsal segments triangular, first segment of hind tarsus subequal in length to second. Pygidium with incomplete basal margin, not reaching side margins (fig. 109). Pygidial disc shagreened, sericeous, impunctate. Total length 4.5-5.5 mm.

Sexual dimorphism. — Male: Fore spur distally expanded and emarginate (fig. 118). Last abdominal sternite shortened medially. Female: Fore spur gradually narrowing distally to dull point (fig. 114).

Type. — Macoucheri, Dominica. USNM.

Remarks. — This species is much more closely related to vitraci of Guadeloupe than to sylvaticus of Dominica. However, it may easily be told from vitraci by the characters mentioned in the key, plus the difference in the form of the female fore spur.

Ecology. — This is a species of lowland coastal forest and scrub. It was collected in an area of tall natural grass and scrub on a steep slope near the sea, in highly xerophytic scrub, and in a patch of moist, shady woods (most abundantly in the latter). Its altitude range on the leeward side of Dominica is 0-800 ft, but only two specimens were collected much above sea level. The species is thus heavily concentrated at sea level and hence allopatric with Ps. sylvaticus of the highlands. One specimen was seen active at 19:30 hrs



Figures 124-128. Fig. 124, Pseudocanthon chlorizans (Bates), &. Fig. 125, Pseudocanthon iuanalaoi n. sp., &. Fig. 126, Pseudocanthon vitraci

(one hour after sunset), indicating that this species is nocturnal. All specimens came to traps baited with cow dung.

Distribution. — Dominica.

Material examined. — 16 specimens. Paratypes are deposited in AM, BMNH, GH, MNHN, USNM.

DOMINICA. St. Joseph Parish: Macoucheri, sea level, 27 May 1964, E. G. Matthews and O. S. Flint (12); .4 mi S of Salisbury, sea level, 27 May 1964, E. G. Matthews and O. S. Flint (1); Clarke Hall (on footpath leading up mountain), 550 ft, 25 May 1964, E. G. Matthews (1); St. Paul Parish: Rodney's Rock (Tarou Point), 200 ft, 25 May 1964, E. G. Matthews and O. S. Flint (1); Greenhill Estate, 800 ft, 3-12 July 1941, R. G. Fennah (1), [USNM].

Pseudocanthon vitraci (Fleutiaux and Sallé), new combination

Canthon vitraci Fleutiaux and Sallé, 1889, Ann. Soc. Ent. France, ser. 6, vol. 9, p. 394; Leng and Mutchler, 1914, Bull. American Mus. Nat. His., vol. 33, p. 438; Blackwelder, 1944, United States Nat. Mus. Bull. 185, p. 202; Balthasar, 1939, Fol. Zool. Hydrobiol., vol. 9, p. 226.

Opiocanthon vitraci (Fleutiaux and Sallé), Paulian, 1947, Coléoptères des Antilles, vol. 1, p. 30.

Description. — Broadly oval, black, sericeous, with legs and antennae pale rufous. Head surface extremely finely and sparsely punctate and shagreened. Dorsal ocular areas large, separated by a distance equal to 5½ times their width at base. Pronotal surface extremely finely punctate, the punctures sparse and barely visible, and strongly shagreened, giving the whole a dull, silky sheen. Median lobe of metasternum finely punctate. Elytral striae indistinct, impunctate. Intervals flat, distinctly shagreened, sericeous, and extremely finely punctate, each puncture bearing an extremely short seta, visible only in oblique light. Fore tibiae with outer distal teeth prominent, the inner margin strongly expanded opposite outer teeth in both sexes (fig. 115). Inner longitudinal carina of upper surface of tibia complete. Femora extremely finely punctate, anterior edge of hind femur margined. Tarsal segments triangular, first segment of hind tarsus subequal to second (fig. 106). Pygidium with a complete basal margin (fig. 110), the disc shagreened, sericeous, impunctate. Total length 4.5-6.0 mm.

Sexual dimorphism. — Male: Fore spur distally expanded and emarginate (fig. 123). Last abdominal sternite shortened medially. Female: Fore spur parallel-sided for basal half, then abruptly narrowing obliquely to a long point (fig. 115). Last abdominal sternite not shortened medially.

⁽Fleutiaux and Sallé), &. Fig. 127, Pseudocanthon j. jamaicensis n. sp., &. Fig. 128, Pseudocanthon sylvaticus n. sp., &.

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Type. — Guadeloupe. MNHN.

Remarks. — Through the courtesy of Dr. Descarpentries the author was able to examine the holotype of this species, which was found to agree perfectly with the five specimens collected on Guadeloupe by the author. This probably marks the first time this species has been re-collected since the days of Vitrac.

Ecology. — This is a species of moist forest at low elevations. It was found in a *Terminalia catappa* association right on the edge of the sea and in inland moist forests up to 1,100 ft elevation. It was not found in the xerophytic forests of Grande Terre, in cow pastures, or high up (3,000 ft) in the humid forest of La Soufrière. Vitrac collected it at "Trois Rivières, sous les détritus de végétaux humides, au bord de la rivière la Coulisse, en mars, et Savanne de l'habitation Grand' Maison, sous une roche" (Fleutiaux and Sallé, 1889).

Distribution. — Guadeloupe.

Material examined. — Six specimens, including holotype. The author's material is deposited in BMNH, GH, and USNM.

GUADELOUPE. *Basse Terre:* Trois Rivières, Coulisse, March, Vitrac (1, holotype), [MNHN]; 6 km S of Goyave (near Ste. Marie, windward coast), sea level, 5 June 1964, E. G. Matthews (3); 5 km W of Vernou (on new road west from Prise d'Eau), 800 ft, 4 June 1964, E. G. Matthews (1); Sofaïa (end of secondary road southwest from Ste. Rose), 1,100 ft, 4 June 1964, E. G. Matthews (1).

Pseudocanthon jamaicensis jamaicensis n. sp.

Description. — Oblong-oval, black, glossy, the legs pale brown. Head surface moderately punctate, the surface between punctures very finely shagreened or smooth. Dorsal ocular areas small, separated by a distance equal to seven times their width at base. Pronotal surface coarsely and evenly punctate, the surface between punctures very finely shagreened. Metasternum evenly, coarsely punctate. Elytral striae distinct but impunctate and superficial. Intervals flat, very finely shagreened and extremely finely and sparsely punctate, each puncture bearing a very short seta. Fore tibiae with outer distal teeth prominent, inner margin slightly bent in at middle (fig. 116). Inner longitudinal carina of upper surface of tibia complete. Femora impunctate or very finely punctate, anterior edge of hind femur margined. Tarsal segments triangular, the first segment of hind tarsus slightly longer than second (fig. 105). Pygidium with complete basal carina, the disc very superficially punctate and shagreened. Total length 3.5-4.5 mm.

Sexual dimorphism. — Male: Fore spur bifurcate, the inner prong acute (fig. 119). Last abdominal sternite shortened medially. Female: Fore spur tapering evenly to a point (fig. 120). Last abdominal sternite not shortened medially.

Type. — 14.5 mi E of Kingston, Jamaica. USNM.

Pseudocanthon jamaicensis viridescens n. subsp.

Description. — Differs from Ps. j. jamaicensis in the following respects: Interpunctural surfaces more distinctly shagreened, giving body a sericeous (not glossy) sheen. Body surfaces with greenish or bluish tinge, seen best in strong natural light. Legs dark, of same color as venter of body. Male fore spur with inner prong lobular, not acute (fig. 121). Female fore spur with inner edge angulate (fig. 122). Total length 4.2-4.7 mm.

Type. — Aberdeen, District of Look Behind, Jamaica. USNM. Intermediates between the two subspecies were collected near Port Antonio and in the Santa Cruz mountains. Intermediates from Port Antonio have the body surfaces glossy but bright green, the male fore spur intermediate in shape, and that of the female like *j. jamaicensis*. The legs are pale. Intermediates from the Santa Cruz mountains are nearly black in color with the legs usually dark, but with some palelegged specimens. Body surfaces are moderately glossy. The fore spurs of both sexes are intermediate in shape.

Remarks. — This species is very closely related to Pseudocanthon perplexus (Leconte) of Mexico and the southern United States, from which it can be distinguished only by the presence of the basal carina of the pygidium and the shape of the fore spur, which is narrower and more clearly bifurcate in the male of perplexus, and simply acute in the female. Ps. j. viridescens differs further from perplexus in the form of the female fore spur and the shagreening of the body surfaces. Ps. jamaicensis is also quite similar to Ps. iuanalaoi n. sp. of St. Lucia, from which it differs primarily in its smaller size, less rotund shape, and more symmetrically bifurcate male fore spur.

Ecology. — The subspecies Ps. j. jamaicensis appears to be confined, in its typical form, to the very dry southeastern belt of Jamaica, where the rainfall is less than 30 inches annually (fig. 129). It occurs in xerophytic forest and scrub. The intermediates from the Santa

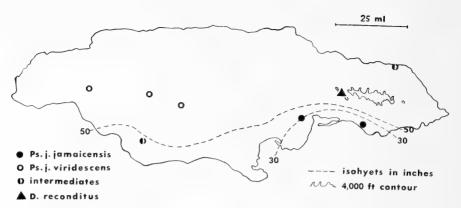


Fig. 129, Distribution of the subspecies of *Pseudocanthon jamaicensis* n. sp. and *Drepanocerus reconditus* n. sp. in Jamaica in relation to rainfall and altitude factors. Isohyets are from Taylor (1956).

Cruz mountains occur in an area of about 50 inches of annual rainfall in xerophytic forest, while the San Antonio intermediates and the typical Ps. j. viridescens all occur in areas of higher annual rainfall, in moist forests. The type locality of the latter consists of dense forest on a steep-sided limestone hill, or "cockpit," on the edge of the Cockpit Country. There appear to be altitude differences between the distributions of the two forms as well, as all jamaicensis and the Port Antonio intermediates were collected at sea level, while all typical viridescens were collected at 800-1,500 ft. However, the Santa Cruz intermediates occur at 200-2,200 ft. The species as a whole was not found above 2,200 ft, or in open land. Much more collecting of this species is necessary to clear up its ecological distribution pattern, which appears to be complex. Unfortunately the species is very elusive. The author set 64 traps in 26 localities throughout the island within the ecological and altitudinal range of the species, and collected it only in 11 traps in seven localities.

All but one specimen collected came to human excrement. One came to a decaying snail, indicating slight necrophagous tendencies in the species.

Distribution. — Jamaica.

Material examined. — 43 specimens. Paratypes of both subspecies are deposited in AM, ANSP, BMNH, CNC, GH, MNHN, SMIJ, USNM.

JAMAICA. *St. Thomas Parish:* 14.5 mi E of Kingston, sea level, 14 January 1947, G. B. Thompson (1), [SMIJ]; 6 October 1964,

E. G. Matthews and T. H. Farr (1); 12 October 1964, E. G. Matthews (5); St. Catherine Parish: Jamaica School of Agriculture, 11 mi W of Kingston, sea level, 29 February 1964, T. H. Farr (1), [SMIJ]; 12 October 1964, E. G. Matthews and T. H. Farr (3) (jamaicensis); Portland Parish: 3.5 mi E of Port Antonio, sea level, 30 July 1965, E. G. Matthews (3); St. Elizabeth Parish: Santa Cruz Mts, miles 10.5, 11, and 16 Black River — Malvern road, 200-2,200 ft, 1 August 1965, E. G. Matthews (8) (jamaicensis × viridescens); 1 mi N of Aberdeen Dist. of Look Behind, 1,000 ft, 31 July 1965, E. G. Matthews (13); Manchester Parish: Grove Place, Agriculture Ministry Farm, 1,500 ft, 11 October 1964, E. G. Matthews and T. H. Farr (3); Westmoreland Parish: 1 mi E of Withorn, 800 ft, 2 August 1965, E. G. Matthews (5) (viridescens).

Genus CANTHON Hoffmannsegg

Canthon Hoffmannsegg, 1817, Entomologische Bemerkungen, Zool. Mag., vol. 1, p. 38.

Nesocanthon Pereira and Martínez, 1956, Rev. Brasileira Ent., vol. 6, p. 105. New synonymy.

Type of genus. — Scarabaeus pilularius Linnaeus, 1758: of Nesocanthon: Canthon callosus Harold, 1868.

Description. — Moderately large beetles (7-22 mm long), variable in surface texture and coloration. Edge of clypeus emarginate or with two or four teeth. Dorsal ocular areas delimited by a nearly complete canthus posteriorly. Posterior edge of head above strongly and completely margined. Antennae nine-segmented. Labium wider than long, very deeply emarginate, labial palpi with basal segment the largest. Pronotum not margined basally, its lateral margins angular or arcuate, their basal portions not appearing subparallel when viewed from above, usually produced backward into prominent hind angles in direct dorsal view. Anterior angles quadrate or acute. Anterior part of prothorax below not excavated to receive fore femora, with or (usually) without a carina running across propleuron. Mesosternum very short and transverse, more than 10 times as wide as long. Meso-metasternal suture evenly and very feebly arcuate. Median lobe of metasternum finely margined laterally. Elytra with nine striae, which are often obsolescent or effaced. Striae 5 and 6 basally approximated. Fore tibia obliquely truncate, with three outer teeth, inner edge evenly curved or nearly straight, not bent, expanded, or dentate. Ventral surface of hind femur with or without a margin paralleling and close to anterior edge. Hind tibiae nearly quadrate in cross section, the lower outer edge medially expanded. Tarsal segments flattened, triangular or trapezoidal, first segment of hind tarsus longer than second. Tarsal claws feebly to moderately curved, not dentate or angulate basally. Abdominal sternites impunctate. Pygidium with a complete basal carina separating it from propygidium.

Distribution. — The Neotropical Region (\pm 150 species), Nearctic (six). In the Antilles (four species): Hispaniola, Grenada. Recorded here for the first time from Grenada.

Remarks. — As restricted in recent works (e.g. Halffter, 1961), Canthon includes only a small number of species in North America (eight), however, the genus seems to be of ancient penetration into that continent because it has given rise to groups restricted to the Mexican Plateau (subspecies of C. humectus Say) and even the eastern United States (pilularius species-group) (Halffter, 1964). In the Antilles Canthon has invaded by two routes: from South America only as far as Grenada, and from an unknown direction to Hispaniola, to which it is restricted in the Greater Antilles.

The three Hispaniolan species, which are clearly derived from a common ancestor, were united in a separate genus Nesocanthon by Pereira and Martínez (1956). On reading their description of Nesocanthon the present writer can find only the following features to distinguish it from Canthon: elytra with uneven surface, pygidium and antennal clubs yellowish, and restriction to Hispaniola. A comparison with Xenocanthon Martínez and Anisocanthon Martínez and Pereira (the only genera with which Nesocanthon is compared) appears artificial to the writer, being based only on the sharing by all three of an uneven elytral surface. Actually, the Hispaniolan Canthon violaceus (Olivier) has only moderately undulated elytral surfaces, only slightly more so than many continental species of the genus. The yellow pygidium is achieved by rendering the disc transparent and allowing the Malpighian tubules to show through (fig. 135). While the position of this pale area may be unusual, the presence of pale whitish areas, achieved by rendering the cuticle transparent, is a common feature of many canthonines.

The Hispaniolan species are somewhat unusual within the genus *Canthon* in possessing the following additional features (not all pointed out by Pereira and Martínez, *op. cit.*): the demarcation between the gula and submentum is very strongly V-shaped or Y-shaped (figs. 137-139), the pronotum has a more or less distinct pre-scutellary impression, the fore spur of both sexes is bifurcate, and the male parameres have no projections (fig. 132). However, the first two features are seen in *Canthon obliquus* Horn at least, and the third feature is seen in some polymorphic *C. indigaceus* Leconte

(Halffter, 1961). Taken as a whole, the characteristics of the Hispaniolan species of *Canthon* do not appear to the present author to be even remotely distinct enough to justify their separation into a different genus.

The above description of the genus is somewhat modified from that of Halffter (1961). Added is the feature of the margined hind edge of the head. The most important modification is the elimination of the requirement that the hind femora be margined on the anterior edge. The Antillean species of *Canthon* fit the description of Halffter in all but this respect, which by itself cannot be decisive. In any case, the above generic description, and all others, must remain provisional until all the South American species of the genus have been re-examined.

C. perseverans n. sp., of Grenada, is not at all related (within the genus) to the Hispaniolan species, and represents a separate penetration from quite a different stock.

Key to the Species of Canthon of the Antilles

- 1. Uniformly dark in color; dull; dorsal ocular areas large, separated by about six times their width. Grenada. perseverans n. sp.
- 2(1'). Pronotum uniformly dark in color (fig. 130); pre-scutellary impression shallow; elytra only moderately callused basally and along sides, the surface merely undulated. violaceus (Olivier).
- 3(2'). Pronotum largely yellow with a large median basal dark area and one smaller darker spot at middle of each lateral and anterior edge (fig. 142); line between gula and submentum in form of normal V, not very deep (fig. 139); lateral margins of pronotum evenly rounded: ventral surfaces of femora impunctate; pygidial disc strongly gibbous.

 signifer Harold.

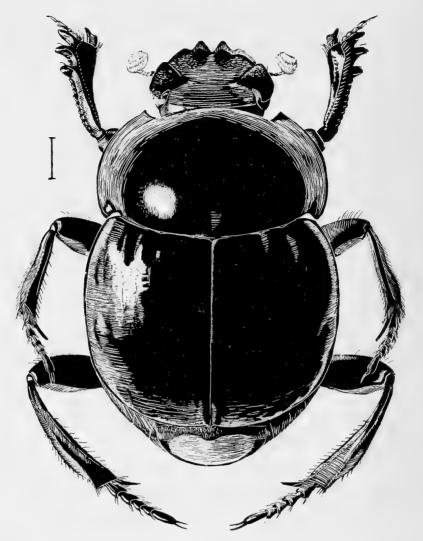


Fig. 130, Canthon violaceus (Olivier), ¿.

Canthon violaceus (Olivier)

Scarabaeus violaceus Olivier, 1789, Entomologie, vol. 1, p. 171; 1790, Encyclopédie méthodique, vol. 5, p. 178; Fabricius, 1798, Supplementum entomologiae systematicae, p. 35.

Ateuchus violaceus (Olivier), Fabricius, 1801, Systema eleutheratorum, vol. 1, p. 65.

Canthon violaceus (Olivier), Harold, 1868, Berliner Ent. Zeit., vol. 12, p. 20; Leng and Mutchler, 1914, Bull. American Mus. Nat. His., vol. 33, p. 438; Chapin, 1934, Proc. Biol. Soc. Washington, vol. 47, p. 101; Balthasar, 1939, Fol. Zool. Hydrobiol., vol. 9, p. 186; Blackwelder, 1944, United States Nat. Mus. Bull. 185, p. 202.

Nesocanthon violaceus (Olivier), Pereira and Martínez, 1956, Rev. Brasileira Ent., vol. 6, p. 107.

Description. — Oval, moderately convex, entirely deep violet-black except antennal clubs and pygidial disc, which are yellowish white. Head surface dull, sericeous, rest of body surface brilliantly shiny. Clypeus with four approximated, rounded teeth, the middle ones much larger (fig. 130). Median ventral process of clypeus a simple transverse fold, not prominent. Head surface impunctate, anteriorly rugulose, posteriorly finely shagreened, sericeous. Dorsal ocular areas separated by a distance equal to 22 times their width at base. Line between gula and submentum in form of an extremely deep V (fig. 137). Lateral margins of pronotum fairly evenly rounded, converging anteriorly (fig. 130). Entire pronotal surface impunctate, smooth, mirrorshiny. Elytral striae nearly obsolete, impunctate. Interstriae flat, impunctate, smooth and shiny. Intervals 2-3 and 5 convex basally, forming, with humeral callus, a series of three indistinct basal calli or undulations on elytra. Anterior and middle femora punctate on ventral surfaces, hind femur smooth. Middle and posterior femora with a row of strong bristles along anterior edge. Anterior edge of hind femur not margined. Tarsal segments subtriangular, first segment of hind tarsus subequal to second (very slightly longer) (fig. 134), claws large, not strongly curved. Pygidium with a faint but complete basal carina separating it from propygidium. Pygidial disc smooth, impunctate. Cuticle of disc and portion of propygidium completely transparent, underlain by a layer of closely coiled strands, probably Malpighian tubules (fig. 135). Aedeagus with parameres evenly tapering, without projection (fig. 132). Total length 8-13 mm.

Sexual dimorphism. — Male with slightly shortened last abdominal sternite, pygidium slightly longer than that of female.

Type. — Santo Domingo. MNHN.

Remarks. — This is the least modified of the Hispaniolan Canthon and shares major features of form and color with typical diurnal species of the continent, such as C. indigaceus Leconte. However, it differs from these in a number of structural details as discussed under the remarks for the genus.

Ecology. — C. violaceus is extremely common in open terrain such as pastures and roadsides in the Dominican Republic, and it occurs chiefly in the lowlands. It may also be trapped in numbers in xerophytic forest; 72 individuals came to a single human fecal

trap under these conditions. Individuals were observed flying in the heat of the day and rolling balls, both singly and in pairs. Ball-making and rolling behavior appears to be identical to that of diurnal *Canthon* of the continent. In Haiti this species is well known to the human inhabitants and is called "Zégué" (Wolcott, 1927).

Distribution. — Hispaniola, evidently widespread throughout the island. The collection of the U. S. National Museum has two specimens bearing the label "Porto Rico, August 1920, G. N. Wolcott." These are probably some of the specimens unsuccessfully released on Puerto Rico from Hispaniola. The species never became established in Puerto Rico (Wolcott, 1922).

Material examined. — 379 specimens.

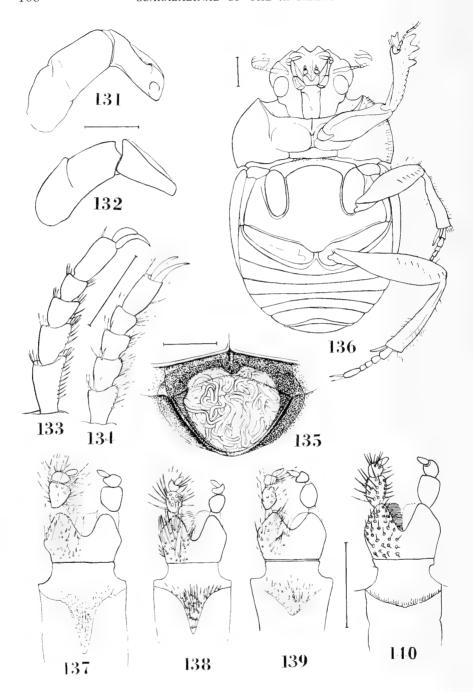
HISPANIOLA. DOMINICAN REPUBLIC. La Romana: La Romana, W. V. Tower (1), [USNM]; Higüeral, 16 April 1913, J. R. Johnston (4), [USNM]; San Pedro de Macorís: San Pedro de Macorís, 28 March 1913, R. G. Russell (1), [USNM]; Distrito Nacional: Boca Chica, Sta. 41, 14 September 1935; R. E. Blackwelder (2), [USNM]; Villa Mella, 1 May 1959, (1), [GH]; 23 km NW of Santo Domingo, 200 ft, 13 October 1964, E. G. Matthews (15); Peravía: 5 km W of Baní, 200 ft, 15 October 1964, E. G. Matthews (74): La Vega: Constanza, 24-27 May, A. Wetmore (5), [USNM]; Santiago: 33rd Ca. [?], Santiago, 22 March 1919, H. B. Sherman (1), [GH]; Santiago, 17 May 1919, H. B. Sherman (4), [GH], [USNM]; 20 mi SW of Santiago, sta. 38, 9 September 1935, R. E. Blackwelder (5), [USNM]; Jánico, sta. 34, 6 September 1935, R. E. Blackwelder (15), [USNM]; Santiago, sta. 40, 10 September 1935, R. E. Blackwelder (2), [USNM]; Santiago, 27 March 1936, S. de Rosario (9), [USNM]; Espaillat: Moca, April 1928, G. Russo (1), [USNM]; J. Gómez M. (3), [USNM]; Puerto Plata: 10 mi SE of Puerto Plata, sta. 36, 8 September 1935, R. E. Blackwelder (20), [USNM]; location not determined: San Francisco Mts., Aug. Busck (19), [USNM]; no further data: S. Dom. (4), [BMNH]; HAITI: Grande Goâve, 20 August 1935, Starr (1), [USNM]; Vieux Bourg d'Aquin, 24 May 1929, Orcutt (113), [BMNH], [USNM] Jérémie, April 1917 (2), [USNM]; Port-au-Prince, Wickham (16), [USNM]; E. A. Klages (1), [USNM]; R. J. Crew (4), [USNM]; M. La Selle, Sta. 22, 8 August 1935, R. E. Blackwelder (6), [USNM]; Kenscoff, sta. 23, 23 August 1935, R. E. Blackwelder (6), [USNM]; 1 mi W of Pétionville (Morne l'Hôpital), sta. 29, 25 August 1935, R. E. Blackwelder (9), [USNM]; Gros Morne, 1926, E. C. Leonard (1), [USNM]; Trouin, sta. 24, 13 August 1935, R. E. Blackwelder (2), [USNM]; Furcy, July-September 1942, A. Curtiss; St. Marc, 1926, E. C. Leonard (2), [USNM]; W. M. Mann (1), [USNM]; 15 mi S of St. Marc, sta. 25, 15 August 1935, R. E. Blackwelder (4), [USNM]; Mirebalais, sta. 31, 1 September 1935, R. E. Blackwelder (4), [USNM]; Pilate, 1926, E. C. Leonard (1), [USNM]; Port-de-Paix, 25 October 1923, (1), [USNM]; La Vallée, Ile de la Tortue, E. C. and G. M. Leonard (2), [USNM]; location not determined: Jean Rabel, January 1929, E. C. and G. M. Leonard (2), [USNM]; Diquini, W. M. Mann (2), [USNM]; Trou Forban, 12 September, A. Curtiss (1), [USNM].

Canthon callosus Harold

Canthon callosus Harold, 1868, Berliner Ent. Zeits., vol. 12, p. 21; Leng and Mutchler, 1914, Bull. American Mus. Nat. His., vol. 33, p. 438; Chapin, 1934, Proc. Biol. Soc. Washington, vol. 47, p. 101; Balthasar, 1939, Fol. Zool. Hydrobiol., vol. 9, p. 186; Blackwelder, 1944, United States Nat. Mus. Bull. 185, p. 198.

Nesocanthon callosus (Harold), Pereira and Martínez, 1956, Rev. Brasileira Ent., vol. 6, p. 107.

Description. — Oval, moderately convex, shiny black or dark brown with slight red-bronze and metallic green reflections especially on head and sides of pronotum. Antennal clubs white. Two large areas on pronotum laterally near base red (fig. 141), these areas sometimes greatly reduced. Sides of median lobe of metasternum and extreme sides of abdominal sternites with reddish areas. Disc of pygidium yellow. Clypeus with two large triangular teeth separated by a V-shaped emargination. Head margin strongly convex behind teeth and obtusely angulate just behind clypeo-genal suture. surface entirely, irregularly rugose and shagreened, with some unevenness and a short transverse carina on frontal surface. Dorsal ocular areas separated by a distance equal to 20 times their width. Line between gula and submentum in the form of a very deep V (fig. 138), but not as deep as in violaceus. Lateral margins of pronotum when viewed from above obtusely angular, the angles a little behind the middle (fig. 141). Entire pronotal surface smooth, shiny, impunctate, but with a callus just in front of lateral fossa. Base of pronotum near margin with a deep pre-scutellary impression. Elytral striae obsolescent. Elytral surface impunctate, smooth and shiny. Bases and sides of elytra blistered, the surface very strongly distorted, forming three basal and three lateral blisters, rest of surface relatively even. Ventral surfaces of middle and hind femora finely punctate, median femur with a few coarse punctures



bearing bristles. Anterior edges of femora with a few short bristles distally. Anterior edge of hind femur not margined. Tarsal segments subtriangular, first segment of hind tarsus very slightly longer than second, subequal. Claws large, very feebly curved. Abdominal sternites finely shagreened, each with a transverse row of indistinct, setigerous punctures laterally. Pygidium with a complete but faint, rounded carina separating it from propygidium. Pygidial disc only mildly convex, impunctate. Aedeagus as in *violaceus* (fig. 132). Total length 5.5-9 mm.

Distribution. — Haiti. Most localities are on the southern peninsula and near Port-au-Prince, but two (Port-de-Paix and Pilate) are in the north.

Material examined. — 25 specimens, including one paratype.

HISPANIOLA. HAITI: Port-au-Prince, R. J. Crew (7), [USNM]; E. A. Klages (4), [USNM]; Wickham (3), [USNM]; August 1924, G. N. Wolcott (1), [USNM]; (1), [BMNH]; Grande Goâve, sta. 28, 20 August 1935, R. E. Blackwelder (7), [USNM]; Gonave I., 18 July 1927, S. T. Danforth (1), [USNM]; Port-de-Paix, 19 January 1925, E. C. and G. M. Leonard (2), [USNM]; Pilate, 10 February 1926, E. C. Leonard (1), [USNM]; no further data: 1935, Blackwelder (1), [USNM]; NO LOCALITY: (1 paratype), [MNHN].

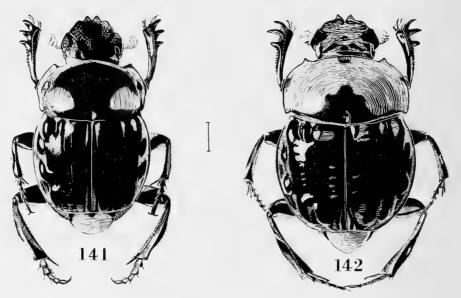
Canthon signifer Harold

Canthon signifer Harold, 1868, Berliner Ent. Zeits., vol. 12, p. 22; Leng and Mutchler, 1914, Bull. American Mus. Nat. His., vol. 33, p. 438; Chapin, 1934, Proc. Biol. Soc. Washington, vol. 47, p. 101; Balthasar, 1939, Fol. Zool. Hydrobiol., vol. 9, p. 183; Blackwelder, 1944, United States Nat. Mus. Bull. 185, p. 201.

Nesocanthon signifer (Harold), Pereira and Martínez, 1956, Rev. Brasileira Ent., vol. 6, p. 107.

Description. — Oval, moderately convex. Head, elytra, and legs, and most of underside, deep chocolate brown, shiny. Pronotum yellow with a large, trilobed mid-basal brown area and three smaller brown spots at middle of lateral edges and anterior edge, entire margin brown (fig. 142). Antennal clubs white. Pygidial disc, center of metasternum, and a spot at lateral edge of each abdominal sternite, yellow. Clypeus with two large, triangular teeth

Figures 131-140. Fig. 131, Canthon perseverans n. sp., aedeagus. Fig. 132, Canthon violaceus (Olivier), aedeagus. Fig. 133, Canthon perseverans n. sp., hind tarsus. Fig. 134, Canthon violaceus (Olivier), hind tarsus. Fig. 135, Canthon violaceus (Olivier), pygidium. Fig. 136, Canthon violaceus (Olivier), ventral view. Fig. 137, Canthon violaceus (Olivier), labium. Fig. 138, Canthon callosus Harold, labium. Fig. 139, Canthon signifer Harold, labium. Fig. 140, Canthon perseverans n. sp., labium.



Figures 141-142. Fig. 141, Canthon callosus Harold, \circ . Fig. 142, Canthon signifer Harold, \circ .

separated by a deep V-shaped emargination. Head margin strongly convex behind teeth and obtusely angulate just behind clypeo-genal suture. surface impunctate, shiny, anteriorly rather irregularly rugulose. Surface of frons somewhat uneven, with a low median gibbosity. Dorsal ocular areas separated by a distance equal to 20 times their width. Line between gula and submentum in form of a V, not deep (fig. 139). Lateral margins of pronotum when viewed from above evenly rounded, converging anteriorly. Entire pronotal surface smooth, impunctate. Base of pronotum near margin with a deep pre-scutellary impression. Elytral striae obsolete, elytral surface impunctate, smooth, and very shiny. Bases and sides of elytra blistered, the surface very strongly distorted, forming three basal and three lateral blisters on each elytron, plus minor irregularities along suture. Ventral surfaces of femora impunctate. Middle and hind femora with a few short bristles on anterior edge distally. Anterior edge of hind femur not margined. Tarsal segments subtriangular, first segment of hind tarsus very slightly longer than second, subequal. Claws large, very feebly curved. Abdominal sternites impunctate. Pygidium with a faint but complete basal carina separating it from propygidium. Pygidial disc strongly swollen, smooth, very finely punctate, with very short setae. Aedeagus as in violaceus (fig. 132). Total length 6.0-8.3 mm.

Type. — Santo Domingo. Not found in MNHN.

Remarks. — This species was not collected by the present author. Wolcott (1927) refers to it as rare in Haiti, and very few specimens

seem to have been collected.

Distribution. — Haiti. The few available exact records are all from the vicinity of Port-au-Prince.

Material examined. — Five specimens.

HISPANIOLA. HAITI: Port-au-Prince, R. J. Crew (2), [USNM]; (1), [USNM]; Pétionville, 30 August 1924, G. N. Wolcott (1), [USNM]; St. Dom. (1), [BMNH].

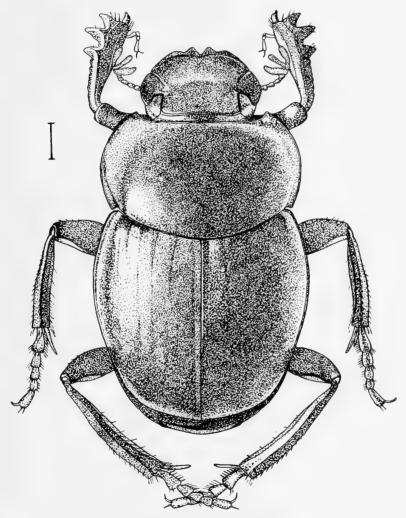


Fig. 143, Canthon perseverans n. sp., 8.

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Canthon perseverans n. sp.

Description. — Elongate oblong-oval, somewhat flattened, uniformly black with slight reddish-purple tinge and faint greenish reflections on anterior part of clypeus, all dorsal surfaces sericeous, dull, legs rufo-piceous, antennae fulvous. Clypeus with two approximated, rounded teeth, separated by a rounded V-shaped emargination and flanked by two shallow emarginations (fig. 143). Head surface very finely shagreened, impunctate, the anterior part of clypeus strongly and irregularly rugose. Dorsal ocular areas large, the distance between them equal to only six times their width at base. Labium normal for genus (fig. 140), line between gula and submentum feebly angulate. Lateral margins of pronotum strongly and evenly rounded in dorsal view (fig. 143). Entire pronotal surface impunctate, very finely shagreened, sericeous. Mesosternum about 10 times as wide as long at middle, meso-metasternal suture evenly arcuate. Metasternum impunctate. Elytral striae very indistinct, impunctate, the intervals flat, impunctate, very finely shagreened, sericeous. Fore legs normal for the genus, distal edge of fore tibia moderately oblique. Middle and hind femora without a row of strong bristles along anterior edges. Hind femur ventrally sparsely punctate, each puncture with a short bristle, anterior edge not margined. Tarsal segments subtriangular except first and last, which are trapezoidal. First segment of hind tarsus distinctly longer than second, about 1½ times as long (fig. 133). Claws strong, moderately curved. Pygidium with strongly angular basal carina. Disc impunctate, sericeous, with a median longitudinal pleat or faint ridge. Aedeagus somewhat broadened and rounded apically, with a strong, rounded lateral subapical projection (fig. 131). Total length 8.2-11.0 mm.

Sexual dimorphism. — Male: Fore spur moderately long and evenly bifurcate. The pygidium is barely longer than that of female, hence last abdominal sternite is only very slightly narrowed medially. Female: Fore spur simple, tapering.

Type. — Perseverance Estate, Grenada. USNM.

Remarks. — This species does not key out either in Harold's (1868d) or Balthasar's (1939) keys to the species of Canthon, nor does it come close to any described species. The canthonine specialists G. Halffter and A. Martínez, who examined specimens of this species, both independently concluded not only that it is a new species, but that it should form the basis for a separate, new and monotypic genus. Both specialists emphasize that it cannot be placed in Canthon as presently conceived.

The present author's belief that *perseverans* fits well within the genus *Canthon*, as described above, stems from his different evaluation of the rank of genus in a taxonomic hierarchy. While admitting

the existence of the various points of difference between the new species and the canthonine genera as presently described, the present author does not consider these differences to be at the generic level of distinction, but perhaps at the level of the species-group (see also remarks under the genus *Canthon*).

The presence of an endemic, and apparently taxonomically highly isolated, species in Grenada is surprising in view of the fact that all the other scarabaeine species there are either continental forms or forms widespread over other islands and taxonomically only slightly differentiated from continental species.

Ecology. — This species appears to be strictly confined to woodlands, both xerophytic and mesophytic, at altitudes from sea level to 500 ft and probably a little higher. It does not occur in the montane forests of the interior, which were sampled at 1,800-1,900 ft, nor is it found in open terrain such as pastures. This latter factor may explain why H. H. Smith overlooked this species when he collected on Grenada in 1889 to 1891, although the large size of the beetle and its great abundance (in forests) still make this oversight rather puzzling. It was not collected by Blackwelder, either. The trapping yield for this species in lowland forests was nearly 14 beetles per trap, using human excrement as bait. Two specimens came to a trap baited with a dead anole, indicating that the species has slight necrophagous tendencies. The large size of the dorsal ocular areas indicates it to be a nocturnal form.

Distribution. — Grenada.

Material examined. — 97 specimens. Paratypes are deposited in AM, ANSP, BMNH, CNC, GH, MNHN, USNM.

GRENADA. St. George Parish: Perseverance Estate, 5 mi N of St. George's, sea level, 8 July 1965, E. G. Matthews (41); Snug Corner, 3 mi NE of St. George's, 500 ft, 8 July 1965, E. G. Matthews (13); Grande Anse, 3 mi S of St. George's, sea level, 8 July 1965, E. G. Matthews (32); St. David Parish: Westerhall Estate, sea level, 9 July 1965, E. G. Matthews (11).

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ERRONEOUS RECORDS

The following additional species are listed from the Antilles other than Trinidad in Leng and Mutchler (1914, 1917) and Blackwelder (1944, 1957). The presence of these species in the Antilles proper has not been confirmed by any recent collecting and their names should be struck off Antillean lists.

Onthophagus bidentatus Drapiez (=femoralis Kirsch). Cited from Guadeloupe as femoralis Kirsch by Fleutiaux and Sallé (1889). The specimens seen by Fleutiaux and Sallé are actually O. antillarum Arrow, according to Paulian (1947). The two species are closely related.

Onthophagus totonicapamus Bates. A Central American species cited from Puerto Rico by Blackwelder (1957). This record is based on a single specimen in the U. S. National Museum bearing the label "Coamo Springs, P.R., April 1899, O. F. Cook." No species of Onthophagus has been collected in Puerto Rico since then; the specimen is probably mislabelled.

Canthidium melanocephalum (Olivier). Cited from Guadeloupe by Olivier in the original description. In Harold's (1867) revision of Canthidium this species is noted to occur only in Brazil and to be fairly common in collections. No mention is made of Guadeloupe in connection with this species by Harold or any one else who has subsequently collected the species, and no Canthidium has been collected in Guadeloupe.

Dichotomius triangulariceps (Blanchard). Cited from Ste. Croix. The origin of this citation is unknown to the author. Ste. Croix was carefully surveyed by the present author and no Scarabaeinae were found there.

Glaphyrocanthon acutus (Harold). Cited by Harold (1868d) as occurring in "Insel St. Thomas." St. Thomas was carefully surveyed by the present author and no Scarabaeinae were found there.

Canthon indigaceus chevrolati Harold. Cited from Hispaniola. The origin of this citation is unknown to the author.

Canthon lituratus Germar. Cited by Harold (1868d) as occurring in the Antilles, possibly referring to Trinidad. It is not known to occur in the Antilles proper.

Canthon muticus Harold. Listed from St. Thomas by Harold (1868d). The same remarks apply as for G. acutus above.

LIST OF THE SCARABAEINAE OF THE ANTILLES

As a result of the previous additions and deletions the list of the known Scarabaeinae of the Antilles now stands at 40 species and five subspecies, as follows. (Synonyms are not listed here.)

Onthophagus marginatus Laporte
Onthophagus a. albicornis Palisot
Onthophagus a. capitatus Laporte
Onthophagus antillarum Arrow
Onthophagus batesi Howden and Cartwright
Onthophagus bituberculatus (Olivier)
Oniticellus cubiensis Laporte
Drepanocerus reconditus n. sp.
Phanaeus carnifex (Linnaeus)
Ateuchus illaesum (Harold)
Ateuchus luciae n. sp.
Uroxys productus Arrow

Uroxys trinitatis Arrow

Uroxys vincentiae Arrow

Canthochilum baracutey Zayas and Matthews Canthochilum tureyra Zayas and Matthews Canthochilum cemi Zayas and Matthews Canthochilum histeroides (Harold)

Canthochilum guayca Zayas and Matthews Canthochilum anacaona Zayas and Matthews

Canthochilum gundlachi (Harold)

Canthochilum pijirigua Zayas and Matthews

Canthochilum h. hispidum Chapin Canthochilum h. iunceanum Matthews Canthochilum h. serropunctae Matthews

Canthochilum oakleyi Chapin

Canthochilum boringuensis Matthews

Canthochilum andyi Chapin Canthochilum taino n. sp. Canthonella pygmaea (Harold) Canthonella isabellae n. sp. Canthonella constans n. sp. Canthonella p. parva Chapin

Canthonella p. luquillensis Matthews Pseudocanthon chlorizans (Bates) Pseudocanthon iuanalaoi n. sp. Pseudocanthon sylvaticus n. sp. Pseudocanthon caeranus n. sp. Cuba

Dominican Republic

Haiti

Lesser Antilles Martinique Martinique Cuba, Jamaica Jamaica Jamaica

Lesser Antilles St. Lucia Guadeloupe

Grenada, Grenadines,

Puerto Rico
Cuba
Hispaniola
Hispaniola
Puerto Rico
Puerto Rico
Puerto Rico
Puerto Rico

Grenada, Grenadines

St. Lucia Dominica Dominica

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Pseudocanthon vitraci (Fleutiaux and Sallé)	Guadeloupe
Pseudocanthon j. jamaicensis n. sp.	Jamaica
Pseudocanthon j. viridescens n. subsp.	Jamaica
Canthon violaceus (Olivier)	Hispaniola
Canthon callosus Harold	Haiti
Canthon signifer Harold	Haiti
Canthon perseverans n. sp.	Grenada

PART II. ZOOGEOGRAPHY

This part will deal with the historical and, especially, ecological factors which have affected the Antillean distribution of the subfamily Scarabaeinae. No attempt is made to formulate general principles or to extend the discussion beyond the Scarabaeinae.

The scarabaeine faunas of the Greater and Lesser Antilles are of completely separate origin and do not come into contact. No direct interchange has occurred between them. The two regions can therefore be treated quite separately.

The Greater Antilles

The genera and the numbers of species of Scarabaeinae in the Greater Antilles are distributed in the following manner (Table 1).

Table 1. — Distribution of genera and numbers of species of Scarabaeinae in the Greater Antilles.

Genus	Jamaica	Hispaniola	Cuba	Puerto Rico	Totals
Phanaeus	1				1
Drepanocerus .	1				1
Oniticellus	1*		1*		1
Pseudocanthon	1				1
Onthophagus			1		2
Canthonella		22	1		4
Canthochilum .			8	5	13

^{*} The same species.

It will be noted that 1) the scarabaeine fauna as a whole shows a great reduction in comparison with adjacent continental areas, such as Central America, which is comparable in both area and climate, and which has over 20 genera and hundreds of species; 2) no genus occurs on more than two islands except *Canthonella*; 3) only in the genus *Canthochilum* and, to a far lesser extent, *Canthon* and *Canthonella*, has there been any insular adaptive radiation, the other genera being represented by but a single species on each island; 4) the fauna of Jamaica stands apart from that of the other islands.

Of the four genera occurring on Jamaica, only one is found on another island (*Oniticellus*; Cuba, Bahamas), but this is represented by the same species on all the islands and it could well be a late migrant from Jamaica to Cuba (or vice versa). This species, *Oniticellus cubiensis* Laporte, is the only one of the Greater Antillean Scarabaeinae found on more than one island and found outside the Greater Antilles, since it occurs in the Bahamas. It is also the only representative of the subfamily in the Bahamas. Thus, if we except this rather ubiquitous species, the Jamaican fauna is virtually unique. The other three islands share elements to varying degrees, without displaying consistent patterns.

Faunistically, the genera break down in the following manner: 1) Genera endemic to the Antilles: Canthonella, Canthochilum; 2) Old World genera endemic to the Antilles in the New World: Oniticellus, Drepanocerus; 3) genera not endemic to the Antilles: Onthophagus, Phanaeus, Pseudocanthon, Canthon. The genera in the first group above are of uncertain affinities and not clearly related to the present continental fauna. Those in the second group are clearly of Asian (i.e., Holarctic) origin in the New World, while, of those in the third group, one (Onthophagus) is also of Asian origin, and only the remaining three (Phanaeus, Pseudocanthon, and Canthon) are clearly of Neotropical origin. Thus, the clearly Neotropical elements of the Antillean scarabaeine fauna are in the minority, comprising three genera and five species, while the elements of certain or possible Old World origin comprise five genera and 23 species — a complete reversal of the ratio seen on the continent, where Neotropical elements are very much in the ascendancy in both Central and parts of North America.

What is the origin of the Holarctic elements of the Antillean scarabaeine fauna? The author believes they came from North America, probably by way of Central America, having reached the former from Asia by the Bering "bridge". The present distribution of *Onthophagus*, with a minimal penetration of South America (where

its place is occupied by the Neotropical Canthidium), is clearly North American in the New World. The oniticelline genera are now unrepresented on the continent, but the tribe is represented by three species of Liatongus which show an unmistakable relict distribution in North America only. No guess can be made as to the origin of Canthochilum and Canthonella. The author believes they are of extremely ancient (early Cenozoic) penetration in the Antilles and are either of Holarctic or of Neotropical origin, more probably the former.

With regard to the Neotropical elements, it is important to note that they are now present on Jamaica (*Phanaeus, Pseudocanthon*) and Hispaniola (*Canthon*) only, suggesting that Jamaica was the "port of entry" for these genera and perhaps all the others, Hispaniola being the next step, then Cuba and Puerto Rico. The last two islands would thus be the last to be affected by new invasions, and would preserve early elements for the longest time (e.g., *Canthochilum*).

Both the taxonomic relationships and the ratio of Neotropical to Holarctic elements of the Greater Antillean scarabaeine fauna suggest to the present observer that this fauna is a greatly reduced sample of the North or Central American fauna of the distant past, perhaps of the Miocene or Pliocene, just after the establishment of the Panama "bridge," when invasion by South American elements was just beginning. Thus, according to the present author's interpretation, the unquestionably high degree of endemicity of the Greater Antillean scarabaeine fauna is a reflection, not of special insular evolution, but of the continued survival of an ancient fauna for which these islands have become a refuge. This survival would not have been possible if the Scarabaeinae were capable of rapid over-water dispersal, in which case new (Neotropical) elements would have swept over the Antilles, displacing the ancient North American elements as they have largely done on the continent.

The Virgin Islands form part of the Greater Antilles geologically (Schuchert, 1935), being separated from the Lesser Antilles by the deep Anegada Passage (Ste. Croix has only recently shifted to the other side of the passage, according to Schuchert (op. cit., p. 474). However, no Scarabaeinae are found on St. Thomas or Ste. Croix (searched by the author), or reported from any other Virgin island.

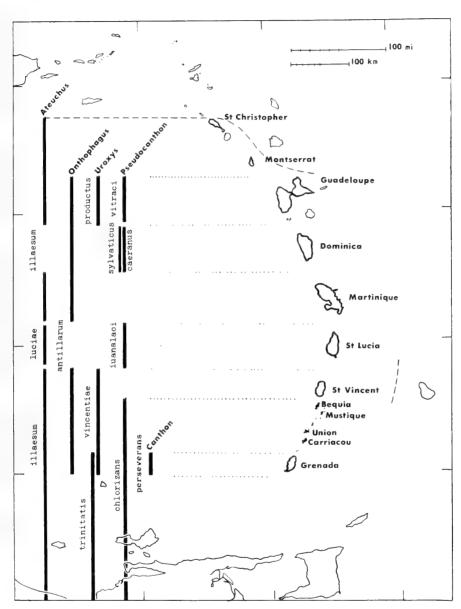


Fig. 144, The Lesser Antilles showing positions of the Volcanic Caribbees and limits of penetration of scarabaeine genera.

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The Lesser Antilles

The Lesser Antilles are divided geologically into the older Limestone Caribbees of late Cretaceous origin but submerged in the Oligocene (Schuchert, 1935), and the True or Volcanic Caribbees, of Oligocene, Miocene, or even more recent origins and never wholly submerged. The Limestone Caribbees are, from north to south, Sombrero Islet, Dog, Anguilla, St. Martin, St. Bartholomew, Barbuda, Antigua, Grande Terre, Désirade, Petite Terre, and Marie Galante. Only St. Martin and Grande Terre were searched by the author. Nothing was found on St. Martin and no Scarabaeinae have been reported from any of the Limestone Caribbees except Grande Terre, which is contiguous with Basse Terre (Guadeloupe).

On the other hand, at least one species of Scarabaeinae occurs on every one of the Volcanic Caribbees, with the possible exceptions of St. Eustatius and Saba (the outermost ones). Fig. 144 shows the known limits of penetration of each genus in the Lesser Antilles, and it may be seen how the Limestone Caribbees and Virgin Islands together form a zone devoid of Scarabaeinae between the faunas of the Greater Antilles and the Volcanic Caribbees. Table 2 gives the distribution of the species in the Lesser Antilles (excluding the two introduced species of *Onthophagus* in Martinique).

It will be seen from the map and table that there is but one species of each genus on any given island with only two exceptions: two species of *Uroxys* occurring on Grenada and two of *Pseudocanthon* on Dominica. It can also be seen that the exclusive island endemics tend to be concentrated on the outermost islands, beginning with St. Lucia. Conversely, one exclusive island endemic, *Canthon perseverans* n. sp., occurs on the nearest island, Grenada. All the species which are common to more than one island, or to the continent and one or more islands, show an "immigrant pattern" of distribution, that is, there is a gradual reduction in the numbers of these species as we move outward from the continent. These species, indicated by X's in table 2, presumably represent a more recent wave of immigration, the exclusive island endemics representing earlier waves.

Table 2. — Distribution of the naturally-occurring species of Scarabaeinae in the Lesser Antilles.

Species	Continent	Grenada	Grenadines	St. Vincent	St. Lucia	Martinique	Dominica	Guadeloupe	Montserrat	St. Christopher
Ateuchus illaesum	X	X	X	X		X		X	X	X
Ateuchus luciae					O					
Onthophagus antillarum		X	X	X		X	X	X		
Uroxys vincentiae		X	X	X						
Uroxys trinitatis										
Uroxys productus								O		
Pseudocanthon chlorizans	X	X	X							
Pseudocanthon iuanalaoi					O					
Pseudocanthon sylvaticus							O			
Pseudocanthon caeranus							O			
Pseudocanthon vitraci								O		
Canthon perseverans		O								
Totals	3	6	4	3	2	2	3	4	1	1

O = Exclusive island endemics.

Distance from the continent is not the only factor determining the numbers of species present on an island, although it is the most important. Island size is evidently influential also, as shown by the relatively rich fauna of Guadeloupe, the largest island of the region (Guadeloupe is actually two islands of different geological history joined together).

While all the scarabaeine species of the Lesser Antilles are clearly derived from South American forms, or identical with them, a fair degree of taxonomic divergence has occurred among the outermost species of *Pseudocanthon* (*sylvaticus*, *caeranus*, and *vitraci*) and the Grenadan *Canthon perseverans*. This morphological divergence has been accompanied by a similar ecological adaptation in all these instances: an adaptation for an exclusive deep-forest existence and probably nocturnal activity, from the original scrubland, and presumably diurnal, immigrants.

The Greater and Lesser Antilles share two genera of Scarabaeinae: *Onthophagus* and *Pseudocanthon*, but there is no indication that these represent any direct faunal interchange between the two regions. It

is more likely that the similarity between the *Pseudocanthon* of Jamaica and St. Lucia (see taxonomic part) represents descent from a common ancestor which was once widespread on the continent and which invaded both Jamaica and the Lesser Antilles separately.

ECOLOGICAL FACTORS AFFECTING DISTRIBUTION ON ISLANDS

A previous analysis of the distribution of the Canthonina of Puerto Rico (Matthews, 1965) showed that altitude changes are the most important environmental factors governing the distribution of these beetles. In general, a species will be found from one end of the island to the other, but only within circumscribed altitude limits. Three distinct altitude distribution belts for these beetles were recognized in Puerto Rico. One species, termed eurytopic, was found to occur at all altitudes, but to show considerable morphological variation in correlation with altitude (this species was referred to as *Canthochilum histeroides* [Harold], but is actually *C. taino* n. sp.).

The importance of altitude factors was found to hold for all other islands investigated, but not to the same extent or with the same type of pattern. In the first place, Puerto Rico is unique in having no species adapted to live in open terrain. Where such species are found, they are seen to be less affected by altitude changes than the forest-dwelling species. Thus *Oniticellus cubiensis* Laporte and *Phanaeus carnifex* (Linnaeus) in Jamaica — species adapted to open lands — may be found from sea level to over 2,000 ft elevation. *Onthophagus albicornis* Beauvois in Hispaniola occurs from sea level to over 4,000 ft. *O. antillarum* Arrow in the Lesser Antilles reaches 2,400 ft — in all cases without showing any altitudinal variation. All these species, however, are more abundant at lower elevations.

In the Lesser Antilles, we can roughly divide the environment into two superimposed belts: the lowland belt $(0-\pm 1,000 \text{ ft})$, of relatively xerophytic evergreen or seasonal forest and scrub, with moister areas along river valleys, and the highland belt $(\pm 1,000-\pm 3,000 \text{ ft})$ of moist or humid evergreen forest, often termed rain forest (Hodge, 1954) although not showing the stratification of the continental rain forests. There is also a higher zone of montane thicket and cloud forest which does not concern us here, as it does

not harbor Scarabaeinae as far as we know. The species which invade open land (pastures, etc.) are all derived from the lowland forest belt. Conversely, species restricted to higher elevations are invariably also restricted to forests. These "rules" probably apply throughout the Antilles in the Scarabaeinae.

It is significant that in the Lesser Antilles the upper belt of humid forest is practically uninhabited by Scarabaeinae. On Dominica there is a species (Pseudocanthon sylvaticus n. sp.) adapted, and restricted, to the rain forest belt from 1,400 to 2,800 ft or more and on Grenada there is a continental species (probably Uroxys trinitatis Arrow) found at 1,600 ft. Aside from these two, no species of Scarabaeinae is known to be able to inhabit the montane forests in the Lesser Antilles. It is also significant that these two cases represent the only instances in the Lesser Antilles where more than one species of a single scarabaeine genus occur on the same island, the other species of the same genus occupying the lowland belt. On all the other islands studied in the region, there is only one species of each genus and it occupies the lowland belt, leaving the upper one unoccupied. We thus see on the two islands mentioned above the initial stages of the process of altitude partitioning of terrain by closely related species — a process developed to a high degree in Puerto Rico, presumably because of the much greater amount of time which has been available for evolution of the fauna there. A corollary to the above observation is that the highland humid forest belt is not invaded except under the pressure of interspecies competition, perhaps resulting from the new invasion of a second species of the same genus. One of the two species may then be displaced upward into the montane zone.

Among the scarabaeine species of the Lesser Antilles we can distinguish ecologically between those restricted to highland forests (the two mentioned above), those occurring both in lowland forests and pastures (Ateuchus illaesum [Harold] and Onthophagus antillarum Arrow), and those restricted to lowland forests (all remaining eight species). The two introduced species of Onthophagus on Martinique occupy a special category of species apparently restricted to pastures. St. Lucia is unique in the island chain in not having any pasture species at all, both Ateuchus illaesum and Onthophagus antillarum being absent.

To summarize, we can compare the Lesser Antilles with Puerto Rico by noting that the former have two altitude distribution belts, of which the upper is barely occupied on two islands and of which the lower may contribute some pasture species, while Puerto Rico has three belts, all of which are occupied by species restricted to them and by the single eurytopic species, none of which invade pastures.

Passing now to the other islands of the Greater Antilles, in Jamaica we return to an ecological situation more similar to that of the Lesser Antilles than to that of Puerto Rico, curiously enough. The upper montane forest belt, or belts, above 2,000 ft are scarcely occupied by Scarabaeinae. Only the localized *Drepanocerus reconditus* n. sp. is truly an upland forest form. Traps set in highland forests in Jamaica generally give negative results. Among the lowland forms there is one (*Pseudocanthon jamaicensis* n. sp.) restricted to forests and showing geographical variation, one occurring in both forests and pastures (*Phanaeus carnifex* [Linnaeus]), and one restricted to pastures and other open terrain (*Oniticellus cubiensis* Laporte). The latter is the only natural species so restricted in the Antillean region, and it indicates the presence of natural savannas before the advent of man.

In Cuba we see a situation beginning to approach a continental pattern, with strong faunal differences between one end of the island and the other. In the genus Canthochilum, with eight Cuban species, the fauna of Oriente province is completely different from that of the rest of the island (see remarks under the genus Canthochilum in Part I and the discussion of island distributions which follows). It should be recalled that Cuba is vastly larger than Puerto Rico (\pm 40,000 sq. mi. vs 3,400) and has a more temperate climate with more pronounced seasonal fluctuations.

Hispaniola also shows strong faunistic differences between the eastern and western ends, with only one taxon out of seven known to be common to both parts (see discussion in following section). There are climatic differences between the northeast and southwest of the island, due to the prevailing northeast winds, but the same differences are also seen in Puerto Rico. The east-west qualitative faunal differences seen in Hispaniola would thus seem to be due either to sheer distance, or to a previous temporary isolation of the two regions.

In sum, no common distributional patterns can be discerned in the scarabaeine fauna of the Greater Antillean islands, as they can in the Lesser Antilles. Each island has its own faunistic patterns resulting from peculiar geographical and historical factors.

Aside from the altitude, vegetational, and distance effects just discussed, the only other environmental factor which may affect the distribution of Scarabaeinae on these islands is soil type. Since Scarabaeinae almost invariably bury the food, both for the adult and for the larva, soil texture may be an important feature of the environment. However, edaphic factors are known to be important in only a very few instances. *Phanaeus carnifex* (L.) of Jamaica is most abundant in the areas of *terra rossa*, as discussed in Part I. In Puerto Rico the canthonines avoid sandy soil, even if forested (Matthews, 1965), and in the Lesser Antilles *Onthophagus antillarum* Arrow is not found in sandy soil, where *Ateuchus illaesum* (Harold) may occur (but not exclusively).

ECOLOGICAL FACTORS AFFECTING DISPERSAL AND SPECIATION

As we have discussed, the Antillean species of Scarabaeinae may be divided into roughly two groups ecologically: lowland forms inhabiting largely xerophytic forests and scrub, sometimes also capable of invading pastures, and highland forms inhabiting humid forest. The former group includes a number of species found on more than one island and therefore capable of dispersal across salt water. the Greater Antilles only one species — Oniticellus cubiensis Laporte — is found on more than one island, but in the Lesser Antilles we have Ateuchus illaesum (Harold), Onthophagus antillarum Arrow, Pseudocanthon chlorizans Bates, and Uroxys vincentiae Arrow in this category. All are inhabitants of xerophytic scrub and the first two also of pastures. That is to say, they are able to inhabit areas along the edge of the sea. This gives them not only a greater opportunity to be transported by sea, but also the capability of becoming established on another island when they get there, on the land adjacent to the sea. The very wide dispersal of Ateuchus illaesum may be due to the additional factor that it is capable of nidificating in sandy soil. Humid forest species, while being easily washed out to sea by way of streams and rivers, are less able to become established

on other islands because their biome requirements are not met in the land areas which they first encounter. This factor is probably the most important barrier to their dispersal, and no highland species is found on more than one island, with the exception of *Uroxys trinitatis* Arrow, found on Trinidad and Grenada.

It follows from the above argument that all highland species must be evolved *in situ* from the original lowland colonizers (although not necessarily the ones which are now there). There are several instances where lowland species on adjacent islands are more closely related to each other than either is to the highland congeneric forms on the same island. For instance, *Canthonella isabellae* n. sp., a lowland form from Hispaniola, is much more similar to the Cuban *C. pygmaea* (Harold) than to the Hispaniolan *C. constans* n. sp., a highland form. *Pseudocanthon caeranus* n. sp. of Dominica is closely related to *Ps. vitraci* (Fleutiaux and Sallé) of Guadeloupe, but fairly distinct from *Ps. sylvaticus* n. sp. from the highlands of Dominica.

This pattern should probably be interpreted to mean that the respective highland forms are not evolved from the lowland forms now present on the same island, but rather that the highland forms represent an earlier invasion by the genus and that these earlier colonizers became displaced upward by the new congeneric arrivals from the adjacent island. A corollary of this interpretation is that speciation has not occurred on a given island alone, but has involved prior geographical isolation.

In the area of the large islands of Cuba and Puerto Rico, where there have been extensive adaptive radiations in the genus *Canthochilum*, a similar multi-island speciation mechanism probably operated, as these islands were broken up into smaller ones during the late Mesozoic and early Tertiary (Mitchell, 1954). That this speciation is confined to *Canthochilum* is explained by the present writer by repeating the assumption made previously in this work that *Canthochilum*, probably alone among the Antillean Scarabaeinae, is a very ancient group and has been present in the area a long time, long enough to have been affected by earlier periods of geological unrest.

The only other genus which has been able to speciate extensively, but using the recent geological configuration of the Antilles, is *Pseudocanthon*. This genus has been able to invade eight of the islands (mostly in the Lesser Antilles) via two different routes, producing

six endemic taxa. On the continent *Pseudocanthon* is a relatively insignificant genus of three known species, one of which is also found in the Antilles. This insular success can be explained only by postulating an unusual ability of the genus to cross water gaps.

DISTRIBUTION BY ISLANDS

This section lists the species occurring on each island, primarily to summarize the ecological distribution of the scarabaeine fauna of the islands known to support this group. The islands are listed according to geographical location and the species according to their ecological distribution.

Iamaica

Oniticellus cubiensis Laporte. Confined to lowland pastures and roadsides. Abundant below 1,000 ft elevation, but may occur up to 2,500 ft.

Phanaeus carnifex (Linnaeus). Lowland pastures and forests up to 2,200 ft elevation. More abundant in areas with deep porous soil on the White Limestone Formation (fig. 31).

Pseudocanthon j. jamaicensis n. sp. Confined to lowland forests in the eastern and southern parts of the island (fig. 129).

Pseudocanthon j. viridescens n. subsp. Confined to forests in the central and western part of the island, up to 2,000 ft elevation (fig. 129).

Drepanocerus reconditus n. sp. Known only from one small area near Hardwar Gap in the Blue Mountains at 4,300 ft elevation, in moist forest (fig. 129).

No Scarabaeinae were collected in the very humid forest areas of Jamaica, as exemplified by the vegetation of the John Crow Mountains and sheltered river gorges in the north and center. For its size and ecological diversity, Jamaica is very poor in numbers of species of Scarabaeinae. Furthermore, the trapping yield in forests (0.58 specimens per trap) was the lowest encountered by the author in the entire Antillean region. On the other hand, two species are remarkably well adapted to pasture conditions (the first two above), and this suggests the presence of extensive natural savanna areas before man came.

Hispaniola

Canthon violaceus (Olivier). Pastures and xerophytic forests up to about 1,400 m in Haiti, but apparently much lower in the Dominican Republic. Much more abundant in the lowlands. Ubiquitous on Hispaniola and not forming any geographical races.

Canthon callosus Harold. Ecology unknown. Confined to the western end of the island.

Canthon signifer Harold. Ecology unknown. Confined to the southwestern end of the island.

Onthophagus a. albicornis Palisot. Pastures and forests, abundant in lowlands, becoming rarer at higher elevations up to 4,500 ft. Known only from the eastern and central parts of the island.

Onthophagus a. capitatus Laporte. Ecology unknown. Confined to the southwestern peninsula of Haiti.

Canthonella isabellae n. sp. Lowland moist forest.

Canthonella constans n. sp. Pine forests at over 5,000 ft elevation in the Cordillera Central.

There is evidently a sharp distinction between the faunas of the Haitian and Dominican parts of the island. Only Canthon violaceus is distributed equally on both sides. One species (C. callosus) is confined to Haiti generally and two forms (C. signifer and Onthophagus a. capitatus) appear to be restricted to the southwestern peninsula, while the remaining three taxa are (so far) known only from the Dominican portion. Several more species of Canthonella evidently remain to be discovered.

Cuba

The author did not visit Cuba, but from information supplied by Ing. F. de Zayas the Cuban Scarabaeinae may be arranged ecologically as follows.

Species of pastures and roadsides (islandwide):

Oniticellus cubiensis Laporte

Onthophagus marginatus Laporte

Species of lowland coastal scrub and forest, known only from the western half of the island and the first two also from the north central coast (Camagüey):

Canthochilum histeroides (Harold)

Canthochilum pijirigua Zayas and Matthews

Canthochilum gundlachi (Harold)

Canthonella pygmaea (Harold). Also found in Oriente.

Forest inhabiting species from interior highlands, known only from Oriente province:

Canthochilum cemi Zayas and Matthews

Canthochilum baracutey Zayas and Matthews

Canthochilum tureyra Zayas and Matthews

Canthochilum anacaona Zayas and Matthews

Canthochilum guayca Zayas and Matthews

As discussed under the remarks to the genus Canthochilum, the Cuban canthonines appear to be distributed geographically, with several species known only from one or two mountain ranges and with a great deal of faunal difference between Oriente and the rest of the island (fig. 52). This contrasts with the Puerto Rican canthonine fauna, which is distributed altitudinally, with most species occurring from one end of the island to the other. These differences are due, without doubt, to the isolated and scattered nature of the Cuban mountain ranges, while those of Puerto Rico are concentrated in two or three closely-placed massifs. However, there is undoubtedly some sort of altitude displacement of species in Cuba as well, at least in the Sierra Maestra.

Puerto Rico

Canthonella p. parva Chapin. Low altitude belt.

Canthonella p. luquillensis Matthews. Middle altitude belt of Luquillo Forest.

Canthochilum borinquensis Matthews. Low altitude belt.

Canthochilum andyi Chapin. Middle altitude belt.

Canthochilum oakleyi Chapin. Middle altitude belt in the Cordillera Central.

Canthochilum hispidum iunceanum Matthews. High altitude belt of the Sierras of Luquillo and Cayey.

Canthochilum h. serropunctae Matthews. High altitude belt of the western Cordillera Central.

Canthochilum h. hispidum Chapin. Distribution unknown. Perhaps the high altitude belt of the eastern Cordillera Central.

Canthochilum taino n. sp. All elevations.

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All of the above species are confined to forests. The limits of the low, middle, and high altitude belts depend on the location on the island. These distributions are discussed in detail in Matthews (1965).

We will pass now to the Lesser Antilles from south to north.

Grenada

Canthon perseverans n. sp. Lowland forests up to 500 ft elevation.

Pseudocanthon chlorizans (Bates). Xerophytic forests near the coast.

Uroxys vincentiae Arrow. Xerophytic forest near the coast.

Ateuchus illaesum (Harold). Lowland pastures and forests, not found much above sea level. Occurs in both clay and sandy soils.

Onthophagus antillarum Arrow. Pastures and forests up to 1,000 ft. Not found in sandy soil.

Uroxys trinitatis Arrow. Highland moist forest at 1,600 ft near the Grand Etang.

Grenadines

Pseudocanthon chlorizans (Bates). Carriacou, Mustique, Union, and Bequia. Xerophytic forests.

Uroxys vincentiae Arrow. Carriacou and Bequia. Xerophytic forests.

Ateuchus illaesum (Harold). Carriacou, Mustique, and Bequia. Xerophytic forests and pastures.

Onthophagus antillarum Arrow. Carriacou and Bequia. Xerophytic forests and pastures.

The islands mentioned here are merely those from which the species have been recorded. Undoubtedly each occurs on every one of the Grenadines, which have a scarabaeine fauna more similar to that of Grenada than to that of St. Vincent. This applies even to Bequia, which is but a few miles from St. Vincent. The abundance of the species on Bequia was surprising, the trapping yield averaging over 27 specimens per trap.

St. Vincent

Ateuchus illaesum (Harold). Lowland forests and pastures, up to 600 ft elevation. Clay and sandy soils. Not found in pastures

exposed to winds on windward coast.

Onthophagus antillarum Arrow. Forests and pastures up to 1,500 ft or higher. Clay and loam soils only.

Uroxys vincentiae Arrow. Moist forest at sea level.

No Scarabaeinae were trapped in the humid forest at Montreal at 1,500 ft elevation.

St. Lucia

Ateuchus luciae n. sp. Forests and very shaded, moist pasture up to 1,000 ft. Not found in typical open pastures at sea level.

Pseudocanthon iuanalaoi n. sp. Forests up to 1,000 ft elevation or higher, more common at sea level. Occasionally found in cow dung in open pastures. Extraordinarily abundant.

The presence of two endemic species, and the absence of the widespread *Ateuchus illaesum* and *Onthophagus antillarum* give St. Lucia a unique scarabaeine fauna.

Martinique

Ateuchus illaesum (Harold). Found by the author only in the driest part of the island, in the rain shadow of Mt. Pelé from St. Pierre to Précheur, in cow dung in dry soil, mostly sandy.

Onthophagus antillarum Arrow. Moist pastures from sea level to 2,400 ft (on the south slope of Mt. Pelé), but more common at lower elevations. Very localized.

Onthophagus batesi Howden and Cartwright. Moist pastures. Introduced.

Onthophagus bituberculatus (Olivier). In dry, sandy pastures at sea level north of St. Pierre. Introduced.

The apparent absence of canthonines and the presence of two introduced species of *Onthophagus* characterize the scarabaeine fauna of Martinique. The highland forests in the interior appear to be uninhabited by this group, as all traps set there (in the Morne Rouge range) gave negative results. The lowland forests were not very well surveyed by the author as this was one of the first islands visited and basic distribution patterns were not understood at that time. Additional species may be discovered here.

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Dominica

Onthophagus antillarum Arrow. Lowland moist pastures and forests.

Pseudocanthon caeranus n. sp. Forest and xerophytic scrub at sea level, one specimen found at 550 ft elevation and one at 800.

Pseudocanthon sylvaticus n. sp. Humid forest and montane thicket at 1,400 to 2,800 ft or higher.

Guadeloupe

Ateuchus illaesum (Harold). Not collected by the author.

Onthophagus antillarum Arrow. Lowland pastures. Apparently extremely localized.

Uroxys productus Arrow. Lowland forests. Not collected by the author.

Pseudocanthon vitraci (Fleutiaux and Sallé). Lowland forests. Localized.

Traps set in the humid forest at 3,000 ft elevation on La Soufrière did not yield any Scarabaeinae.

Montserrat

Ateuchus illaesum (Harold). One specimen from this island seen by the author bears the notation "woodlands," the other is from Blackwelder station 262: ". . . on the coast; a small stream. . . . In dung."

St. Christopher

Ateuchus illaesum (Harold). Xerophytic forests and pastures up to 700 ft elevation. More abundant in sheltered areas. Absent from windswept pastures.

The magnificent rain forest occupying the windward slopes of Mt. Misery appears to be devoid of Scarabaeinae.

As Nevis, St. Eustatius, and Saba are close to St. Christopher and similar in topography and history, *Ateuchus illaesum* should be sought on those islands too. Saba, however, has no lowland pasture land.

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